Recent advances in the understanding of ecosystem processes at eddy covariance CO₂ flux sites in East Asian forest ecosystems: a review

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Abstract

To elucidate the dynamic features of carbon sequestration in ecosystems under changing climates and various disturbance regimes, researchers must understand key ecosystem processes, such as carbon allocation and partitioning, organic matter decomposition, and nutrient cycles, as well as plant functional traits. Here, we reviewed the existing literature and conducted meta-analyses using available datasets from eddy covariance CO₂ flux sites in East Asia to clarify these ecosystem processes and attributes. Since the establishment of AsiaFlux in 1999, the number of flux tower sites has grown to 110 sites, spanning a large geographic extent in East Asia and covering diverse ecosystems embedded in large climatic gradients. Early publications relating to AsiaFlux described CO₂ fluxes from single sites, but over the last 20 years more ecosystem processes and attributes have been included in the study sites’ research programs. Among other advances, researchers have quantified the plant functional traits related to photosynthesis or ecosystem-scale gross primary production and thus demonstrated that CO₂ fluxes are controlled by plant traits; this quantification provides a basis for building ecosystem models. Additional means of understanding the carbon fluxes and pools of these ecosystems have been provided by biometric measurements beneath eddy covariance flux towers, partly on the basis of traditional forestry practices and the measurements of component carbon fluxes, such as respiratory fluxes and litter decomposition rates. Through meta-analyses, we demonstrate good correlations between these fluxes and mention the characteristics of carbon cycle processes in Asian forest ecosystems. By investigating nitrogen biogeochemical cycles at the flux sites, studies have shown that carbon fluxes are also controlled by nitrogen availability. The future success and progress of AsiaFlux could be promoted by further collaborations between this research community and other networks, such as long-term ecological research (LTER) networks, and the development of open databases.

Key words: AsiaFlux, Carbon allocation and partitioning, Decomposition, Nitrogen biogeochemical cycle, Plant functional traits

1. Introduction

Climate change is a direct driver causing the global degradation of natural environments, including declines in ecosystem extent, biomass, and species abundance (e.g., Diaz et al., 2019). Despite the fact that anthropogenic greenhouse gas emissions are thought to have exclusively caused climate change, these emissions continue to increase, with the annual emission rate reaching an unprecedented value of 11.5 ± 0.9 Gt C year⁻¹ in the end of the 2010s (Friedlingstein et al., 2019). One core area of interest has therefore centered around trying to understand an ecosystem’s carbon budget and the mechanisms that control it. The community of carbon flux researchers has gradually developed worldwide; a global network of flux measurement sites, FLUXNET, was established in 1998 (Baldocchi et al., 2001), and the AsiaFlux regional network was established in 1999 (Yamamoto et al., 2005). Since then, Asia, with its large population, rapid economic growth, and accompanying enormous greenhouse gas emissions, has shown rapid growth in the number of flux tower sites, which have provided more than 20 years of continuous flux data (Baldocchi, 2020).

Although multiple aerodynamic and vegetation criteria must be fulfilled, eddy covariance observations at these flux tower sites can be used for determining the carbon budget because they provide flux data with a high time resolution (usually every 30 min) for determining the net ecosystem exchange (NEE) rate of carbon dioxide (CO₂) between the ecosystem and the atmosphere, and its subsequent partitioning into gross primary production (GPP) and ecosystem respiration (Rₑ) (Saigusa et al., 2002). At most of the flux tower sites, however, studies have also investigated other ecosystem attributes and processes, as many different factors are equally important for understanding ecosystem functions and are indispensable for explaining the observed flux patterns and building ecosystem models. These
additional efforts often arise from collaborations between scientists from various research disciplines, such as plant ecophysiology, micrometeorology, remote sensing, ecosystem modeling, soil ecology, and biogeochemistry.

To establish a broader view for understanding forest ecosystem carbon budgets, here we review the literature on four ecosystem attributes and processes (Fig. 1): (1) canopy functional traits that are related to or control the ecosystem’s carbon fluxes; (2) carbon allocation and partitioning, which provide a parallel estimation of annual ecosystem carbon budgets; (3) organic matter decomposition, which returns organic carbon back to the atmosphere as CO$_2$ and accumulates the recalcitrant component in humus; and (4) nitrogen (N) biogeochemical cycling, which determines N availability and thus controls the carbon fluxes from GPP all the way through to decomposition in the ecosystem. The scope of this literature review is principally limited to the AsiaFlux and ChinaFLUX sites in East Asia, which cover boreal to tropical regions.

2. Canopy functional traits and carbon fluxes

On the basis of 20 years of flux tower measurements made by the eddy covariance method, data from the AsiaFlux sites offer profound knowledge about the exchange of CO$_2$ and water vapor between ecosystems and the atmosphere (Mizoguchi et al., 2009). Along with quantifying the fluxes, studies have also intensively investigated the major abiotic factors that control the fluxes. Chen et al. (2015) explored the spatial variations of GPP, $R_e$, and net ecosystem production (NEP) at 241 flux sites (67 in Asia, 91 in Europe and Africa, and 83 in North America) in the Northern Hemisphere; they found that the annual carbon fluxes from the three regions were positively correlated with mean annual temperature and mean annual precipitation. On this large spatial scale, the carbon fluxes were also positively correlated with the enhanced vegetation index (EVI), which is a modified normalized difference vegetation index (NDVI) that is sensitive to high biomass regions. These findings suggest that the plants that compose the ecosystems control the carbon fluxes through their functional traits, which include structural, chemical, physiological, and longevity aspects of the leaf economic spectrum, thus allowing scaling to canopy processes of whole ecosystems (Pérez-Harguindeguy et al., 2013). Although local meteorological conditions do influence the magnitude of the ecosystem carbon flux, the long-term variation of the ecosystem carbon flux is controlled by the respective plant traits and their abundances of plants that compose the ecosystem (Stoy et al., 2009).

![Fig. 1. Schematic representation of the ecosystem processes related to eddy covariance carbon fluxes. Dark arrows represent the flow of carbon via gross primary production (GPP); ecosystem respiration ($R_e$), which is the sum of autotrophic respiration ($R_a$) and heterotrophic respiration ($R_h$); litterfall, which transfers aboveground and belowground biomass to soil; and the leaching loss through dissolved carbon. The gray arrows represent N cycling, including the deposition of reactive nitrogen (N$_r$), biological N$_2$ fixation, the emission of gaseous N species from soil, and the leaching of dissolved N. The N fluxes and pools determine the availability of soil N and thus control the vegetation growth (C2). Soil N and the litter N content exert control on organic matter decomposition (C3). The ecosystem GPP is strongly controlled by plant functional traits (C1).](image-url)
2.1 Functional traits correlated with carbon fluxes

In general, temperate ecosystems present a clear annual cycle of growing seasons and dormant seasons. These regular seasonal dynamics determine the temporal variation of the direction of daily NEE from a net source in the dormant season to a net sink in the growing season (e.g., Wang et al., 2004). For deciduous forests, the leaf phenology or leaf area index (LAI) demonstrates how a plant functional trait directly controls the interchange of the seasonality and, therefore, the carbon flux. On the other hand, compared with deciduous forests, evergreen coniferous forests present a steadier LAI level throughout the year and usually have a longer growing season (Ohtani et al., 2005). In a larch forest in Mongolia, the development of the canopy in the growing season resulted in the NEE being linearly correlated with the NDVI; the NDVI, a proxy of LAI, explained 62% of the variation of NEE (Li et al., 2005). In broadleaf Korean pine mixed forest, the seasonal variation of GPP and $R_s$ showed a strong positive correlation with the vegetation absorption index (Zhang et al., 2006a).

A step beyond the influence of LAI on the seasonal variation of carbon fluxes is the investigation of the seasonal variation of plant traits related to leaf morphology, chemical composition, and physiological properties and how they may influence the carbon fluxes at the ecosystem scale. For example, Muraoka and Koizumi (2005) used leaf chlorophyll content and leaf mass per area (LMA) to represent leaf photosynthetic capacity, which was larger in canopy species than in understory species and reached its maximum value later than the LAI did. Leaf-level photosynthetic properties also have been shown to correlate with leaf N concentration. For example, Peltoniemi et al. (2012) used data from 14 flux sites in the Northern Hemisphere (including one AsiaFlux site in Teshio, Japan) and found a linear correlation between maximum light use efficiency (LUE) and leaf N concentration. Consequently, the ecosystem GPP increased linearly with leaf N over a wide range of light conditions.

In addition to these studies of how leaf traits control ecosystem carbon fluxes, Miyama et al. (2003) did pioneering work on in situ continuous measurements of leaf-level carbon flux and compared them with eddy covariance measurements. They found that the diurnal pattern of the net assimilation rate for the leaves enclosed in the automatic leaf chamber coincided well with the NEE measured by the eddy covariance system above the canopy.

2.2 Plant traits used in ecosystem modeling

Simulating the GPP is the core module of ecosystem modeling because it quantifies the amount of carbon entering an ecosystem from the atmosphere. Two widely employed approaches for calculating GPP (Hikosaka et al., 2016) are the biochemical approach, which simulates the reactions between light and carbon during photosynthesis (Ball et al., 1987; Farquhar et al., 1980), and the LUE approach, which calculates GPP by multiplying LUE by absorbed photosynthetically active radiation and then adjusts it by using environmental factors such as temperature and vapor pressure deficit (Yuan et al., 2014). In both kinds of models, functional traits at the leaf and canopy scales are necessary model input parameters.

When biochemical models of photosynthesis are used, leaf-scale photosynthetic characteristics such as the maximum rate of carboxylation ($V_{cmax}$) are used for scaling up to the ecosystem-scale GPP (e.g., Tanaka et al., 2002; Watanabe et al., 2005). Kosugi and Matsuo (2006) measured and normalized dark respiration, $V_{cmax}$, and the stomatal conductance coefficient at 25 °C over 1 year. They found it was important to incorporate the seasonal variation of these normalized parameters when modeling ecosystem photosynthesis. At several other AsiaFlux sites, researchers using field measurements and model simulations have drawn similar conclusions about the importance of incorporating the seasonal variation of plant traits in biochemical models of photosynthesis (Muraoka et al., 2010; Tanaka et al., 2002), especially the changes in leaf traits over the aging process (Ito et al., 2006).

Although the seasonal variation of leaf-level traits has been shown to be related to the seasonal variation of carbon fluxes, the interannual phenology variation may also deserve further attention. Noda et al. (2015) found that two abiotic factors, the growing-degree days and the chilling-degree days, sufficiently explained the variations of functional traits such as chlorophyll content, LMA, light-saturated net assimilation rate, maximum electron transport rate at a reference temperature, and $V_{cmax}$ at a reference temperature. This interesting finding may help researchers explore carbon fluxes under future climate change conditions.

LUE models are widely used in estimating large-scale GPP because of their relatively simple parameterization and the availability of satellite-derived land surface properties. For example, Nakaji et al. (2007, 2008) derived the two main canopy-level parameters for LUE models, the fraction of absorbed photosynthetically active radiation and $ε$ (conversion coefficient of absorbed energy), from satellite-derived NDVI and photochemical reflectance index, respectively. When estimating regional GPP by using a LUE model, He et al. (2014) noticed that the uncertainties of photosynthetically active radiation and the satellite-derived EVI are higher than that of maximum LUE. Although the application of LUE models in the large-scale estimation of GPP has been quite successful, we must consider that satellite images do not give information on the vertical stratification of the canopy, shrubs, and ground vegetation, all of which contribute to ecosystem GPP. Lin et al. (2018) demonstrated that they could significantly improve the simulation of ecosystem GPP by taking into account the traits of different plant “sub-systems.”

With recent advances in machine learning approaches, satellite-derived canopy-level vegetation indices have also been used as input information to predict large-scale carbon fluxes (Ichii et al., 2017).

2.3 Inverted canopy-level traits

Some important physiological properties of plants can be calculated from ecosystem-level carbon flux data. Because these inverted canopy-level traits, or “ecosystem functional properties” (Reichstein et al., 2014), fluctuate less over time compared with the raw 30-min flux data, they may correlate better with plant functional traits. Zhang et al. (2006b) calculated ecosystem-level apparent quantum yield, maximum photosynthetic capacity, and $R_s$ from an eddy covariance dataset and found that the variation...
of these traits between different sites was mainly controlled by temperature and phenology. In another study, Xia et al. (2015) derived the ecosystem-scale phenology (length of CO₂ uptake period) and an ecophysiological property (seasonal maximal capacity of CO₂ uptake and GPPₘₐₓ) from each annual eddy covariance dataset from 213 flux tower sites around the world. They found that the annual GPP could be predicted well by the product of CO₂ uptake period length and GPPₘₐₓ, indicating that these two parameters are useful canopy-level traits.

3. Carbon allocation and partitioning

Although significant advances have been made in understanding forest carbon cycling in East Asian ecosystems during the past several decades (e.g., Hirata et al., 2008; Saigusa et al., 2013), large uncertainties remain regarding fundamental carbon allocation and partitioning processes. Carbon fixed by photosynthesis can be released into the atmosphere by respiration or stored in plant biomass and soil (Fig. 1). As these components have different carbon residence times, carbon allocation and partitioning play a critical role in the carbon cycle in forest ecosystems (e.g., Chen et al., 2013; Litton et al., 2007).

Current in situ measurements of the carbon cycle in forest ecosystems mainly rely on the eddy covariance method and biometric method. The former method provides the following components of the carbon fluxes between ecosystems and the atmosphere.

\[
GPP = R_c = -NEE = NEP,
\]

whereas the latter provides more detailed components of the carbon allocation and partitioning, including net primary production (NPP), autotrophic respiration (Rₐ), soil respiration (Rₛ), heterotrophic respiration (Rₜ), root respiration (Rᵣ), litterfall (L), and biomass increments (ΔB). The relationships among these parameters can be expressed as follows:

\[
GPP = NPP + R_c,
\]

\[
NPP = NEP + R_b = AB + L,
\]

\[
R_c = R_a + R_b,
\]

\[
R_c = R_b + R_r.
\]

In addition to each individual approach, combined analysis and meta-analysis using both eddy covariance and biometric data can provide a deeper understanding of carbon allocation and partitioning in forest ecosystems. In this section, through a literature review, we (1) describe several combined analyses that have been done at the AsiaFlux and ChinaFLUX sites and (2) analyze the Compilation Dataset of Ecosystem Functions in Asia, which is a compilation of annual carbon flux and stock data of each component of forest ecosystems, to clarify carbon allocation and partitioning and their spatial variations from tropical to boreal regions, especially in East Asia.

3.1 Combined analysis using both eddy covariance and biometric data

Over the past two decades, several combined analyses of East Asian ecosystems have been conducted. Ohtsuka et al. (2009) directly compared interannual variations of eddy covariance components (i.e., GPP, Rₐ, and NEP) and those of biometric components (i.e., biometric-based NEP, foliage NPP, woody tissue NPP, and Rᵣ) of a cool-temperate deciduous broadleaf forest in Takayama (TKY), Japan. Interannual variation of NEP was well explained not only by the foliage NPP or Rᵣ but rather by woody tissue NPP. Another study investigated the annual carbon balance by combining long-term forest inventory data with physiological measurement data in an ecological research plot beneath an eddy covariance flux tower in a primary tropical seasonal rainforest in Xishuangbanna, southwestern China (Tan et al., 2010). The study revealed high leaf respiration and low ecosystem carbon use efficiency (CUE) and noted that the allocation patterns were similar to those reported in primary tropical rainforests in the Amazon region. On the other hand, Katayama et al. (2013) found remarkably higher total belowground carbon flux in a Bornean tropical rainforest without dry seasons even though the aboveground NPP in the forest was comparable with the respective values for tropical rainforests in the Amazon.

The change in carbon balance after forest disturbance and forest management is another crucial topic in the East Asian region. Yamanoi et al. (2015) investigated the effects of a windthrow disturbance on carbon balance in a mature secondary deciduous broadleaf forest in western Hokkaido, Japan, and Takagi et al. (2009) studied the carbon balance before and after clear-cutting of a mixed forest in northern Hokkaido, Japan. Both studies found that the ecosystem carbon balance changed from a carbon sink to a carbon source after disturbance or clear-cutting, although the GPP of the understory dwarf bamboo increased with an increase in the plant biomass and photosynthetic activity.

Such combined analyses and datasets have provided useful information for site-specific modeling studies that clarified, for example, the crucial contribution of fine roots to carbon allocation in a cool-temperate forest (Kondo et al., 2015), the carbon and water cycle after typhoon damage in a cool-temperate forest (Toda et al., 2011), and the carbon balance and vegetation structure dynamics along the forest age gradient in Siberian larch forests (Sato et al., 2010).

Another fundamental research topic is the degree of uncertainty in estimates of components in the carbon allocation and partitioning processes. Components such as GPP and NEP can be individually estimated by eddy covariance and biometric methods. Therefore, intercomparisons between the two methods have been conducted in various forest ecosystems, providing useful information on estimate uncertainties (e.g., Hirata et al., 2008; Katayama et al., 2013; Tan et al., 2010).

3.2 Meta-analyses using annual carbon components

Although the relationships between carbon fluxes (GPP, Rₐ, and NEP) and climate conditions have been analyzed through tower flux observations (Chen et al., 2013b; Kato and Tang, 2008; Saigusa et al., 2013), meta-analyses examining detailed components of carbon allocation and partitioning at multiple sites in Asian regions are limited (Kondo et al., 2017). Here, we show the result of an analysis of the Compilation Dataset of Ecosystem Functions in Asia (available upon request from the corresponding author, T.M. Saitoh). For a detailed site description of the 22 forest sites analyzed here, see Kondo et al. (2017).
The relationships between GPP and each respiration and production component in forest ecosystems in East Asia are shown in Fig. 2. GPP ranged from 2.1 to >40 Mg C ha\(^{-1}\) year\(^{-1}\), covering nearly the entire global GPP range (DeLucia et al., 2007; Luyssaert et al., 2007). Each annual respiration component (i.e., \(R_e\), \(R_a\), \(R_h\), \(R_{ab}\), and \(R_r\)) showed a significant linear relationship with GPP (Fig. 2a–e). NPP became saturated as GPP increased in East Asian forest ecosystems (Fig. 2f), although DeLucia et al. (2007) found a clear linear relationship between GPP and NPP in global forest ecosystems that included only an Asian site (NPP = 0.53 × GPP − 11 Mg C ha\(^{-1}\) year\(^{-1}\), \(R^2 = 0.72, p < 0.01\)). Our analysis indicates that NEP could be slightly explained by GPP in any climate zone (Fig. 2g), whereas Kondo et al. (2017) found that GPP in mid- to high-latitude and low-latitude forests was positively and negatively related to NEP, respectively. This result suggests that large GPP does not directly result in large NEP and is comparable with the findings of a meta-analysis at CarboEuro flux sites (Luyssaert et al., 2010).

CUE, which is the ratio of NPP to GPP, is another crucial indicator of carbon partitioning (DeLucia et al., 2007). Our

![Fig. 2. The influence of gross primary production (GPP) on the spatial pattern of (a) ecosystem respiration (\(R_e\)), (b) autotrophic respiration (\(R_a\)), (c) heterotrophic respiration (\(R_h\)), (d) aboveground respiration (\(R_{ab}\)), (e) root respiration (\(R_r\)), (f) net primary production (NPP), and (g) net ecosystem production (NEP) in East Asia. Symbols represent annual values at forest sites. Thick and thin lines represent regression results and 95% confidence intervals, respectively. DBC, boreal deciduous coniferous forests (five sites); TDB, temperate deciduous broadleaf forests (four sites); TEC, temperate evergreen coniferous forests (three sites); STR, subtropical forests (three sites); TRF, tropical rain forests (five sites); MF, mixed forests (two sites).]
meta-analysis revealed that CUE significantly decreases with increasing GPP in forest ecosystems (Fig. 3a). This result is consistent with NPP saturation at higher GPP (Fig. 2f). In addition, on the basis of data for sites where measurements exist for aboveground and total biomass in a forest ecosystem, CUE was significantly negatively correlated with aboveground biomass and total biomass (Fig. 3b, c). These results demonstrate that the partitioning to NPP is not constant across a wide range of GPP values in forest ecosystems and varies with carbon resource availability and maintenance costs of aboveground biomass in East Asian regions under monsoon climate.

There are clear differences in carbon allocation and partitioning among plant functional types, namely, between deciduous and evergreen forests (Fig. 4). The ratio of aboveground respiration to

![Image](image_url)

**Fig. 3.** Spatial relationship of carbon use efficiency (CUE) against (a) gross primary production (GPP), (b) aboveground biomass, and (c) total biomass in forest ecosystems in East Asia. Symbols and lines are the same as in Fig. 2.

![Image](image_url)

**Fig. 4.** Ratios (%) of ecosystem respiration ($R_e$), autotrophic respiration ($R_a$), heterotrophic respiration ($R_h$), aboveground respiration ($R_{ab}$), root respiration ($R_r$), net primary production (NPP), and net ecosystem production (NEP) to gross primary production (GPP) compared between deciduous forests (white) and evergreen forests (gray). Each box indicates average and standard deviation. Each circle indicates the annual value at an individual site. Statistical significance is indicated by ** ($p < 0.01$) and * ($p < 0.05$).
GPP was significantly lower in deciduous forest than in evergreen forest, whereas the ratios of $R_{h}$ and NPP to GPP were clearly greater in deciduous forest than in evergreen forest. These results are partly attributable to differences in the leafy period and its maintenance costs between the two forest types.

Because combined analyses using both eddy covariance and biometric data have been conducted for limited ecosystem types, it is essential to conduct further such analyses, especially in different ecosystems such as wetlands, paddy fields, and mangroves.

4. Organic matter decomposition

In addition to $R_{h}$, the $R_{b}$ of soil organisms is one of the major processes of carbon loss from ecosystems (Chapin et al., 2011). Although soil stores more carbon than vegetation in global terrestrial ecosystems (Cao and Woodward, 1998), one of the largest sources of uncertainty in estimating NEP is $R_{b}$. $R_{b}$ is mostly dominated by decomposition of organic matter such as leaf, woody, and root litter by soil bacteria and fungi. In terrestrial ecosystems, a large fraction of carbon fixed by NPP is released to the atmosphere through $R_{b}$ (Fig. 5a), resulting in a small amount of NEP compared with NPP. Consequently, a slight change in decomposition activity can lead to a large change in carbon stocks and the carbon balance in the ecosystem.

4.1 Components of $R_{b}$

Ecosystem-level $R_{b}$ is strongly correlated with aboveground litter input in forest ecosystems in East Asia (Fig. 5b), suggesting that the largest source of $R_{b}$ is from decomposition of fresh litter (mostly leaf litter). Kominami et al. (2012) reported that approximately 60% of newly supplied leaf litter was decomposed within a year in a warm-temperate forest in Japan. Although few studies have reported the CO$_2$ flux from coarse woody debris in the AsiaFlux sites, it often comprises more than 20% of total $R_{b}$ (Kominami et al., 2008). Because coarse woody biomass is one of the largest carbon sinks of forest ecosystems, this type of biomass turns into a substantial carbon source after a large disturbance or at a late successional stage (Goulden et al., 2011; Yamanoi et al., 2015). Although our understanding of the decomposition of fine roots is still limited compared with that of leaf litter, input of fine root litter often exceeds that of leaf litter (Schulze et al., 1999), suggesting that the fine root component is also a large source of $R_{b}$. One of the greatest sources of uncertainty in predicting the response of $R_{b}$ is the late phase of soil organic matter (SOM) decomposition. As plant litter decomposes, microbially resistant compounds such as lignin, oils, and fats are concentrated in SOM, and stable compounds such as polysaccharides and polyuronids are synthesized through the activities of soil microbes. These resistant SOM components play a role in the long-term carbon budget. Although a few review articles discuss this topic (e.g., Conant et al., 2011), the long-term decomposition dynamics of SOM is yet to be clarified.

4.2 Factors controlling organic matter decomposition

The two major approaches to estimate $R_{b}$ are (1) measurement of the CO$_2$ efflux from materials through the use of chambers and (2) measurement of the mass loss of materials during a given time period (e.g., by using the litter bag technique). In the chamber method, $R_{b}$ is estimated as the integration of all components contributing to $R_{b}$ or, after roots are removed by a trenching technique, as the soil respiration without living root respiration (Hanson et al., 2000). On the basis of the flux measurements using chambers, instantaneous $R_{b}$ is usually modeled as a simple function of temperature or as a function of temperature and moisture. Because the annual carbon flux through decomposition can be easily estimated by the function, most studies that estimate ecosystem carbon flux on the basis of biometric measurements have adopted the chamber method (e.g., Kominami et al., 2008; Ohtsuka et al., 2007; Tan et al., 2010).

Factors that affect the rate of litter mass loss (i.e., the decomposition rate constant $k$ of materials) have been identified by using the litter bag approach, especially for fresh leaf litter. This approach is useful for comparing the mass loss of different materials or in different environmental conditions. The results must be carefully interpreted, however, because litter bag experiments are often carried out in somewhat unnatural decomposition conditions and often fail to quantify processes such as decomposition by macrofauna or physiological leaching.

Previous experimental evidence indicates that the primary factors controlling decomposition of leaf litter are the initial litter qualities, as well as climatic factors such as temperature and moisture (Zhang et al., 2008). Although temperature and
moisture (or actual evapotranspiration) are thought to be good predictors of the litter decomposition rate (Gholz et al., 2000; Tuomi et al., 2009; Zhang et al., 2008), litter qualities often explain more of the variation in decomposition rates than do climatic factors at the regional scale (Bradford et al., 2016; Brovkin et al., 2012; Cornwell et al., 2008). For fresh leaf litter, which is the largest source of \( R_h \), the important factors are the C:N ratio or N content (Cornwell et al., 2008; Freschet et al., 2012; Zhang et al., 2008), leaf dry matter content (= dry mass divided by water saturated mass; Freschet et al., 2012), tannin content (Zhang et al., 2008), and lignin content (Cornwell et al., 2008; Freschet et al., 2012; Prescott, 2005). Decomposition of woody litter, which is slower than that of leaf litter but often becomes a large \( R_h \) source after a large disturbance, is affected by the diameter of logs (Mackensen et al., 2003), wood density (Pietusch et al., 2014), and N content (Weedon et al., 2009). Decomposition of root litter also plays a major role in \( R_h \) because fine roots, like leaves, undergo frequent growth and death cycles, although our knowledge of the decomposition of this component is relatively limited. The important factors in root decomposition are the C:N ratio or N content (See et al., 2019; Silver and Miya, 2001), lignin content (Freschet et al., 2012; See et al., 2019), calcium content (Silver and Miya, 2001), and the mycorrhizal association type (See et al., 2019).

In addition, the plant lifeform and traits relating to the “plant economic spectrum” such as LMA are also important factors, in that the leaf, root, and wood of nutrient-acquisitive species (i.e., species with lower LMA) are more likely to decompose faster than are those of high-LMA species (Cornwell et al., 2008; Freschet et al., 2012). This difference has important implications for trait-based modeling of ecosystem processes because plant traits such as LMA are strongly related to ecosystem production and can also be associated with litter decomposability at the site.

The interaction between climatic factors and litter quality can confound the quantification of climatic factor effects on decomposition because some properties of litter cannot be parameterized and can also change with climate. One approach to isolate the effects of litter quality from those of abiotic factors in comparison across sites is to perform a decomposition experiment using standardized materials. Although several types of standardized materials, such as cotton strips, have been used (Harrison et al., 1988), a unique approach using commercially available tea bags was recently developed (Djukic et al., 2018; Keuskamp et al., 2013). This approach enables researchers to measure how decomposition activity responds to a variety of environmental variables. A regional-scale harmonized decomposition experiment was carried out using the tea bag approach in 87 study plots across Japan (S.-C. Chang et al., 2019). The results showed that the \( k \) value (i.e., the decomposition rate constant obtained from the exponential function of the temporal changes in decomposition) increased linearly with air temperature (Fig. 6), and there was also a large difference between the \( k \) values of different leaf types [Aspalathus linearis [rooibos tea] vs. Camellia sinensis [green tea]]. This result confirmed that climate and litter quality are strong factors that control litter decomposition. However, even with the standardized litter bags, there was still a large variation between sites with similar air temperatures. Because most Japanese forested areas are mesic to humid, humidity seemed not to be a limiting factor. Thus, it appears that other factors such as soil properties and associated soil fauna and microbial communities may affect the decomposition rate.

4.3 Decomposition studies in AsiaFlux

Among the AsiaFlux sites, intensive work on \( R_h \) has been conducted at Yamashiro (YMS), which is located in a warm-temperate forest in Japan. Ataka et al. (2014, 2015) assessed microscale spatiotemporal variation of leaf litter decomposition due to changes in litter water content. Respiration from leaf litter decomposition just after rainfall events (within 1 day) became 8.6-fold larger than that prior to rainfall (Ataka et al., 2014), which indicates that precipitation strongly controlled decomposition. Furthermore, the vertical position within the litter layer also significantly affected leaf litter respiration; respiration from the top position was almost threefold larger than from the bottom position (Ataka et al., 2015). Jomura et al. (2007) directly measured respiration from coarse woody debris of a variety of species using a closed-chamber method and developed a comprehensive decomposition function accounting for several coarse woody debris characteristics (wood density and diameter) at the YMS site. This decomposition function has been used to estimate ecosystem flux (Kominami et al., 2008).

![Fig. 6. Decomposition rate constant (k) of tea leaves versus average August temperature at sites across Japan. Closed circles, green tea; open triangles, rooibos tea. Data from Suzuki et al. (2019).](image-url)
An experimental soil-warming approach was used to clarify the response of soil respiration to warming in a cool-temperate forest at Takayama (TKY) in Japan (Noh et al., 2016, 2017). The results of this study indicated that \( R_\text{p} \) was more sensitive to soil warming as compared to \( R_\text{s} \). Furthermore, the effects of warming on \( R_\text{s} \) slightly decreased during the 4-year experimental period (Noh et al., 2017), suggesting that there are some negative feedback processes between soil warming and decomposition; that is, long-term soil warming might lead to changes in physiological or chemical soil properties, which in turn depress the sensitivity to soil warming.

Uchida et al. (2005) quantified litter decomposition under snow at the TKY site. The mass loss rate of leaves during winter (December to April) reached 13% and accounted for 26% of the annual mass loss. This kind of study on the soil cover on litter decomposition is important for future prediction because the area and length of snow cover will likely change with future climate changes in East Asia.

### 5. Nitrogen biogeochemical cycle

Nitrogen is an essential nutrient for ecosystem productivity and carbon flux, especially in temperate ecosystems, and phosphorus is important in tropical regions (e.g., Vitousek and Farrington, 1997). Therefore, N often limits forest growth, whereas excess N causes negative consequences in ecosystem productivity and functions, with long-term temporal transition of N roles in ecosystems via succession and environmental changes (Aber et al., 1989; Burns, 2004; Groffman et al., 2018; Lovett and Goodale, 2011). Over the last few decades, however, human activities such as fossil fuel combustion and excess use of chemical N fertilizer have increased the global flow of reactive N (\( \text{N}_\text{f} \): all N species except \( \text{N}_2 \)), which, in turn, has caused environmental problems such as air pollution, water eutrophication, soil degradation and acidification, biodiversity loss, ecosystem changes, human health issues, and greenhouse gas (i.e., nitrous oxide, \( \text{N}_2\text{O} \)) emission (Galloway et al., 2008; Kou et al., 2018a; Shibata et al., 2015; Zhou et al., 2016). In this section, we review the current findings from N biogeochemical studies in the AsiaFlux and ChinaFLUX sites and other research sites on forest N cycle in East Asia.

Soil N properties control plant nutrient uptake and photosynthesis, and these processes ultimately supply organic matter (i.e., litterfall and decomposition), nutrients, and energy (e.g., Zhou et al., 2015) to the soil system. Soil microbes play a significant role in N transformation (i.e., mineralization, nitrification, immobilization, and denitrification) driven by various biotic and abiotic factors. Urakawa et al. (2016) analyzed the factors that control soil N mineralization and nitrification at 38 Japanese forest sites, including the AsiaFlux sites, and they found that the content of SOM was a strong factor that explained site-to-site variations in soil microbial N processes. In forest soil systems, these N processes depend on interactions between carbon (as an energy source) and N (as a nutrient). For example, soil N mineralization and nitrification rates are driven by the C:N ratio of the substrate (i.e., litter and SOM), because soil microbes need both energy and N to maintain their metabolism activities and the proper C:N ratio of the microbial biomass (e.g., Aber et al., 1989; Lovett and Goodale, 2011). Therefore, different organic matter C:N ratios among different plant species, or changes in the C:N ratio by alteration of carbon cycles in an ecosystem caused by an increased atmospheric CO\(_2\) concentration, can lead to changes in soil microbial N processes (Lovett and Goodale, 2011).

Soil microbial N transformation produces not only nutrients for plants and microbes but also gaseous N compounds (i.e., \( \text{NH}_3 \), \( \text{NO} \), \( \text{NO}_2 \), \( \text{N}_2\text{O} \), and others), which become a source for the N outflow pathway from ecosystems to the atmosphere (Fang et al., 2015; Gao et al., 2017; Hayashi et al., 2009; Zhou et al., 2016). The emission of \( \text{N}_2\text{O} \) from ecosystems is a significant source of this greenhouse gas, as well as CO\(_2\) and methane (\( \text{CH}_4 \)). Along this line, Gao et al. (2018), on the basis of in situ litter removal experiments, reported that removal of the litter input to a soil system significantly decreased \( \text{N}_2\text{O} \) emissions from soil in tropical rainforest. Hayashi et al. (2009) found significant \( \text{NH}_3 \) emissions from anaerobic forest soil in a larch plantation in northern Japan. Because gaseous emissions of N compounds vary across large spatial and temporal scales and have various driving factors, further research on this topic needs to include meta-analyses and synthesis, based on research site networks such as FLUXNET and the International Long-Term Ecological Research Network (ILTER) (Shibata et al., 2015) and modeling analysis (Tian et al., 2015).

Atmospheric N deposition is an important nutrient source but can also become a source of pollutants when the N supply exceeds the N demand of an ecosystem. Yu et al. (2014) indicated that NEP in Asian forests is enhanced by the increase of atmospheric N deposition as a nutrient supply (Fig. 7). Increased N inputs have the potential to alter various biogeochemical processes of N in ecosystems, resulting in changes in ecosystem structure and functioning. In China, various manipulation experiments have been conducted to clarify the impact of N addition on soil microbial N processes (Gao et al., 2016a, 2016b, 2016c; Kou et al., 2019b), plant N nutrition (Kou et al., 2018a), root growth and dynamics (Kou et al., 2015, 2017a, 2017b, 2018b, 2019a), and greenhouse gas emissions (Gao et al., 2018; Zhao et al., 2018; Zhou et al., 2016). For

![Fig. 7. Relationship between net ecosystem production (NEP) and atmospheric wet N deposition in Asian monsoon forests (redrawn from Yu et al., 2014).](image-url)
example, Zhao et al. (2018) reported that total soil respiration was significantly increased by 16.5% in a high N addition plot (150 kg N ha⁻¹ year⁻¹), whereas Rₑ was significantly decreased by the N addition as a result of the reduction of both microbial biomass carbon and enzyme activity.

6. Conclusions and future perspectives

The 20-year regional network of ecosystem carbon flux research in East Asia has led to substantial progress in understanding the functioning of diverse ecosystems that span the climate spectrum from tropical to boreal zones. The interdisciplinarity collaboration of researchers working within the AsiaFlux network has improved our knowledge of the spatio-temporal patterns of carbon cycles, especially the following ecosystem attributes and processes: canopy functional traits, carbon allocation and partitioning, organic matter decomposition, and the N biogeochemical cycle.

First, mechanistic explanations of the relationships between plant functional traits and carbon fluxes remain a challenge. Nonetheless, the stomatal density (number of stomata per unit leaf area) and stomatal index (proportion of stomata to epidermal cell numbers) have been shown to decrease with increasing atmospheric CO₂ concentration (Yan et al., 2017); this relationship deserves further exploration. Furthermore, studies of plant functional traits have advanced our understanding of not only the role of canopy leaves in carbon fluxes but also those of woody tissue and the relationship between roots and mycorrhizal fungi (e.g., Makita et al., 2009; Sun et al., 2017). More research on plant functional traits would provide useful information for flux research communities.

Second, although several modeling and remote sensing studies over the last decade have used the bottom-up approach to estimate the carbon balance on the national to regional scales in East Asia (Ichii et al., 2013, 2017; Sasai et al., 2016; Yu et al., 2014), the field measurement validation datasets for previous studies have generally been made up of either eddy covariance or biometric data. Therefore, it is essential to perform additional modeling and remote sensing studies that consider carbon allocation and partitioning based on both types of field measurement data. Recently, the NEP concept has been expanded to the net ecosystem carbon balance, which includes additional non-CO₂ fluxes such as leaching, lateral transfers, harvesting, fire, herbivory, CH₄, carbon monoxide, and emission of biogenic volatile organic compounds (Bonan, 2008). As such, the net ecosystem carbon balance concept is suitable for estimates of the regional carbon balance in terms of global climate change, and additional studies of non-CO₂ carbon fluxes in carbon partitioning in forest ecosystems are expected to provide reliable estimates of ecosystem carbon accumulation.

Third, Rₑ, which is an important component of ecosystem flux to predict the response of ecosystem NEP to climate change, has been intensively evaluated by the chamber method at the AsiaFlux sites. Such studies have demonstrated how Rₑ responds to changes in environmental conditions such as temperature and moisture. However, litter bag experiments have suggested that litter qualities strongly affect the decomposition rate. Our understanding of the effects of litter quality on ecosystem-level Rₑ is too limited to develop a complete process-based model of Rₑ.

Climate change can cause changes in species composition, which leads to changes in litter quality. To develop a model to project the response of decomposition to climate change, a quality-based approach is necessary for all components of organic matter, including leaf, wood, and other soil organic materials.

Fourth, interactions between carbon flux and N biogeochemical cycles are complex (e.g., Lovett and Goodale, 2011) and are not yet fully understood, including the linkages to other elements such as phosphorus (Kitayama et al., 2004; Kitayama 2006). This is especially true for Asian regions, where, compared to other regions, spatial and temporal variations of atmospheric N pollution are quite large (Yu et al., 2019) and long-range transport of pollutants occurs across countries (e.g., Morino et al., 2011) and is driven by a wide range of natural and social conditions (Kim et al., 2018). Global and regional cross-site analyses (Mirtl et al., 2018; Shibata et al., 2015) and long-term data analysis (e.g., Groffman et al., 2018) with further consideration of the uniqueness of Asian environmental changes (e.g., typhoons and extreme climate disturbances, volcanic soil and landscape characteristics, and earthquake impacts) would improve our understanding of how N biogeochemical cycles affect carbon flux in forest ecosystems.

Finally, although several functional trait databases (e.g., TRY; https://www.try-db.org/tryWeb/Home.php), ecological databases (e.g., JaLTER database; http://db.cger.nies.go.jp/JaLTER/metacat/style/skins/jalter-en/index.jsp), and data papers (e.g., Scientific Data, Ecology data paper, and Ecological Research data paper) have provided convenient datasets, further developments and improvements in data sharing between disciplines are necessary. Such data sharing would allow for advanced combined analyses and meta-analyses at eddy covariance sites and improve our understanding of ecosystem processes in various types of ecosystems in East Asia.

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