Key Points:
- The observed fine root allocation decreased with increasing temperature and precipitation, but leaf allocation showed an opposite change
- The observed wood and leaf allocation decreased with increasing forest stand age, but fine root allocation showed an opposite change
- Terrestrial biosphere models cannot completely reproduce the observed biogeographical patterns of NPP allocation in forest ecosystems

Correspondence to:
W. Yuan,
yuanwpcn@126.com

Global Patterns in Net Primary Production Allocation Regulated by Environmental Conditions and Forest Stand Age: A Model-Data Comparison

Jiangzhou Xia[1] (iD), Wenping Yuan[2,3,4] (iD), Sebastian Lienert[5] (iD), Fortunat Joos[5] (iD), Philippe Ciais[6], Nicolas Viovy[6] (iD), Ying-ping Wang[7,8] (iD), Xufeng Wang[9] (iD), Haicheng Zhang[6] (iD), Yang Chen[1], and Xiangjun Tian[10] (iD)

[1]Tianjin Key Laboratory of Water Resources and Environment, Tianjin Normal University, Tianjin, China, [2]School of Atmospheric Sciences, Sun Yat-sen University, Guangzhou, China, [3]Zhuhai Joint Innovative Center for Climate-Environment-Ecosystem, Zhuhai Key Laboratory of Dynamics Urban Climate and Ecology, Beijing Normal University, Zhuhai, China, [4]Southern Marine Science and Engineering Guangdong Laboratory, Zhuhai, China, [5]Climate and Environmental Physics, Physics Institute and Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland, [6]Environnement (LSCE), CEA CNRS UVSQ, Gif-sur-Yvette, France, [7]CSIRO Oceans and Atmosphere, Aspendale, Victoria, Australia, [8]South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China, [9]Key Laboratory of Remote Sensing of Gansu Province, Heihe Remote Sensing Experimental Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou, China, [10]International Center for Climate and Environment Sciences (ICCES), Institute of Atmospheric Physics, Chinese Academy of Sciences, Beijing, China

Abstract The allocation of net primary production (NPP) to different plant structures, such as leaves, wood, and fine roots, plays an important role in the terrestrial carbon cycle. However, the biogeographical patterns of NPP allocation are not well understood. We constructed a global database of forest NPP to investigate the observed spatial patterns of forest NPP allocation, as influenced by environmental drivers and forest stand age. We then examined whether dynamic global vegetation models (DGVMs) could capture these allocation patterns. The NPP allocation response to variations in temperature or precipitation was often opposite in leaves and fine roots, a finding consistent with the functional balance theory for allocation. The observed allocation to fine roots decreased with increasing temperature and precipitation. The observed allocation to wood and leaves decreased with forest stand age. The simulated allocation with five DGVMs was compared with the observations. The five models captured the spatial gradient of lower allocation to fine roots with increasing temperature and precipitation but did not capture coincident gradients in allocation to wood and leaves. None of the five models adequately represented the changes in allocation with forest stand age. Specifically, the models did not reproduce the decrease in allocation to wood and leaves and the increase in allocation to fine roots with increasing forest stand age. An accurate simulation of NPP allocation requires more realistic representation of multiple processes that are closely related to allocation. The NPP allocation database can be used to develop DGVMs.

1. Introduction

How plants allocate net primary production (NPP) among different organs profoundly affects plant growth, competition, and the terrestrial carbon (C) cycle (Bonan, 2015; Friedlingstein et al., 1999; Malhi et al., 2011; McMurtrie & Dewar, 2013). In general, NPP allocation affects the C cycle in two ways: first, NPP allocation to leaves or fine roots determines the potential of plants to capture water, nutrients, and light and second, different plant components turn over at different rates, so that allocation to slow turnover organs (e.g., stems) increases the residence time and C storage (Franklin et al., 2012). With the changing climate, NPP allocation in forests has received particular interest because it affects C sequestration and the global C balance (Gim et al., 2017; Guillemot et al., 2017; Li et al., 2016; Montané et al., 2017). For example, a previous study has found high variability (up to 29%) among model estimates of woody biomass depending on different assumptions about the allocation of NPP (Ise et al., 2010).

Although the importance of NPP allocation is clear, there are large uncertainties concerning how it should be modeled. The challenges in developing NPP allocation models mainly relate to three aspects. First, NPP allocation is the outcome of many processes (Cannell & Dewar, 1994; Franklin et al., 2012; Le Roux et al.,

2001). The interaction among individual processes hinders understanding of the NPP allocation process (Franklin et al., 2012). Second, NPP allocation to different plant organs is inherently difficult to measure (Fatichi et al., 2019). A lack of observational data prevents the improvement of existing alternative NPP allocation models. Third, the absence of processes closely related to NPP allocation in the dynamic global vegetation models (DGVMs) impedes the development of allocation models, such as wood phenology and nonstructural carbohydrates. Several improvements have been made in the observation of these processes (Delpierre et al., 2016; Gough et al., 2009; Richardson et al., 2013; Rossi et al., 2016). However, the modeling of these processes in DGVMs lags behind the observations.

In general, vegetation models use either a static or a dynamic NPP allocation scheme. Static NPP allocation models assume constant allocation fractions among plant components for a given plant functional type (PFT). The static NPP allocation models cannot predict the observed allometry among the leaves, wood, and roots (Lloyd & Farquhar, 1996). These static NPP allocation parameters have been found to be highly uncertain and to significantly affect the simulated vegetation carbon fluxes and pools (Pappas et al., 2013; Zaehle et al., 2005). Moreover, substantial spatial and temporal differences in NPP allocation among plant components (De Kauwe et al., 2014; Doughty et al., 2015) within similar plant communities or ecosystem types have been observed, findings contradictory to the static allocation model.

Over the past two decades, global vegetation models have increasingly adopted dynamic allocation schemes that vary the allocation coefficients with ontogeny, environment, and resource availability (McConnaughay & Coleman, 1999; Poorter et al., 2012). Franklin et al. (2012) have reviewed several approaches for modeling NPP allocation in plants. However, allometric relationship and functional balance models are the only major types of dynamic model that have been widely incorporated into global DGVMs (Krinner et al., 2005; Moorcroft et al., 2001; Reyes et al., 2017; Sitch et al., 2003; Spahni et al., 2013; Wang et al., 2010; Xia et al., 2015).

The allometric models use empirical relationships of biomass among plant components to simulate tree height, stem length, diameter, leaf area (LA), carbon reserves, and forest stand volume. In general, two relationships are included in the functional relationship approach: the ratio of leaf to sapwood area (SA; i.e., the "pipe model" theory) and the ratio of root to leaf biomass (Sitch et al., 2003). The functional balance models assume that plants allocate their resources (C and nutrients) to optimize their gain of further resources (including water, light, and soil nutrients) in response to their growth environment (Dewar, 1993; McConnaughay & Coleman, 1999; Thornley, 1972). For example, fine root allocation will increase if water stress increases, because the plant needs more roots to sustain water uptake and growth (Friedlingstein et al., 1999).

Studies have increasingly examined the performance of NPP allocation in relation to observational estimates at the site scale (De Kauwe et al., 2017) or national scale (Guillemot et al., 2017). Furthermore, a study in a tropical forest region has suggested that the NPP allocation schemes used by the Coupled Model Intercomparison Project Phase 5 (CMIP5) Earth system models, including functional balance and functional relationship models, do not accurately represent the observed allocations of NPP in leaves, wood, and roots for tropical forests (Negrón-Juárez et al., 2015). These model evaluations are conducted at local scales or for specific regions, and a comprehensive evaluation over larger areas still is lacking.

The temperature, water, nutrients, and other environmental variables vary substantially worldwide. How the spatial gradients in NPP allocation into plant components are influenced by environmental variables and how those influences are represented in global vegetation models have not been well investigated. In addition, biological regulation, for example, that associated with increasing plant age, is also important in NPP allocation. One common pattern in forest growth is an increase in aboveground wood production early in stand development, after the maximum LA is reached, followed by a declining rate of increase in stand biomass (Gower et al., 1996; Ryan et al., 1997). To understand why models differ in their predictions of C sequestration, and to decrease the uncertainty from NPP allocation, we sought to characterize the assumptions made in different models and to determine whether these assumptions are correct by conducting a model-data comparison.

This study used a global data set on the allocation of NPP in tropical, temperate, and boreal forests to define the spatial patterns in NPP allocation in different plant components. Five DGVMs, incorporating allometric relationship or functional balance allocation approaches, were selected to evaluate model performance in
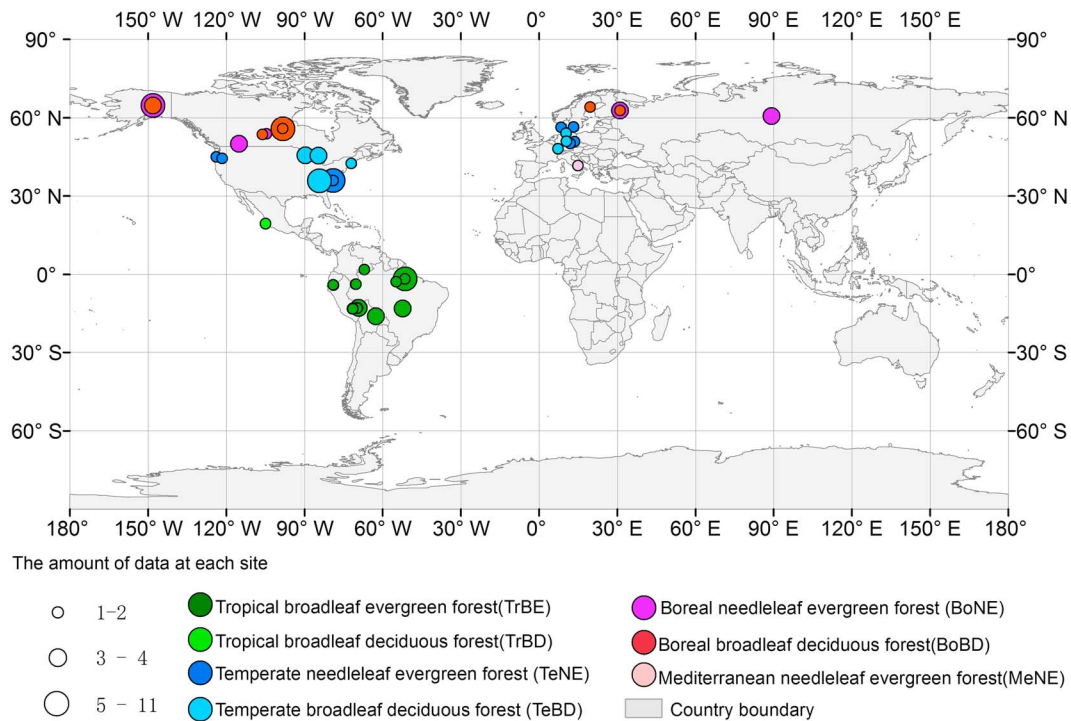
Figure 1. Distribution of the net primary production allocation observations used in this study. The size of the dots corresponds to the amount of data at a given site, and the color indicates the forest ecosystem type.

reproducing NPP allocation patterns. These models have been widely used in global applications and are integrated into Earth system models. Our model-data comparison examined the frameworks and parameter settings of NPP allocation used in these models. Our specific objectives were to (1) investigate biogeographic differences in NPP allocation to wood, leaves, and fine roots; (2) examine the performance of the selected land biosphere models in capturing the observed spatial gradients of allocation in forests; and (3) identify the shortcomings of models in representing key NPP allocation processes.

2. Materials and Methods

2.1. NPP Allocation Data Set

Three criteria were used to select the data for our study: (1) at least three components of NPP, woody production (NPP_{wood}, including stem, branches, and coarse root NPP), leaf production (NPP_{leaf}), and fine root production (NPP_{froot}) were reported; (2) the forest stands were not managed, because forest management would greatly alter allocation of NPP (Campioli et al., 2015); and (3) ancillary site information, such as the year of seedling establishment, observation year, forest age, PFT, longitude, and latitude, were reported. Sites with many years of observations were still considered the same site. Finally, 112 site-years (72 sites) of observations in seven forest types across the global forest were retrieved (Figure 1 and Table S1 in the supporting information). The seven forest types were tropical broadleaf evergreen, tropical broadleaf deciduous, temperate needleleaf evergreen, temperate broadleaf deciduous, boreal needleleaf evergreen, boreal broadleaf deciduous, and Mediterranean needleleaf evergreen forests.

In this study, the observed NPP allocation of global forests was obtained from three data sets. The first data sets were extracted from the latest version (version 3.3.1) of the global NPP database originally collected by Luyssaert et al. (2007; http://www.lsce.ipsl.fr/en/Phocea/Pisp/visu.php?id=124&uid=sebastiaan.luyssaert), which has been updated and corrected by Vicca et al. (2012). The other two data sets included observations at control plots of three free-air CO_2 enrichment sites (Norby et al., 2005) and seven tropical rainforest sites in Amazonia (Doughty et al., 2015). The observed annual NPP allocation fractions to leaves (*aleaf*), wood (*awood*), and fine roots (*aroot*) were calculated as the ratios of annual NPP_{leaf}, NPP_{wood}, and NPP_{froot} to their sum, respectively. More detailed information on the NPP allocation data set can be found in the

supporting information (Aragão et al., 2009; Bascietto et al., 2003; Black et al., 1996; Bond-Lamberty et al., 2004; Comeau & Kimmins, 1999; Curtis et al., 2002; da Costa et al., 2014; Doughty et al., 2015; Girardin et al., 2010; Gough et al., 2007; Gower et al., 2001; Jordan et al., 1999; Kimball et al., 1997; Knohl et al., 2003; Kutsch et al., 2001; Law et al., 2004; Maass & Martinez-Yrizar, 2001; Malhi et al., 2009; Moser et al., 2011; Norby et al., 2001; Ruess et al., 1996, 2003; Ryan et al., 1997; Schulze, 2000; Wirth et al., 2002).

Forest NPP was measured through independent measures of leaf, wood, and fine root production. Leaf NPP was estimated from leaf litter collection. Wood NPP included both the aboveground and belowground components. The aboveground wood NPP included stem and branch NPP. The aboveground wood NPP was estimated with site- and species-specific allometric relations relating stem diameter and tree height to the total aboveground biomass. The belowground wood NPP included only coarse root NPP. The coarse root NPP was estimated through several methods, such as site-specific allometric relations relating tree basal area to root biomass, the ratio of coarse root NPP to aboveground wood NPP, and harvesting (Table S1). Twigs were not included in the aboveground wood NPP. The information in bark was not explicitly reported in the literature but was usually included in stem NPP. The coarse roots were defined as roots with a diameter >2 mm (Cornelissen et al., 2003). The diameter cutoff for the roots was not reported in the literature. The same definition of wood NPP was used for all sites. In general, fine roots were defined as roots with a diameter <2 mm (Cornelissen et al., 2003). In this study, the 2 mm as threshold to classify fine roots was used for 94% of sites, and fine roots were defined as 5 mm at only three sites (Table S1). At more than 90% of sites, fine root NPP was measured through three methods: minirhizotron, soil core and ingrowth core. At 9% of sites, fine root NPP was calculated as fine root biomass multiplied by the fine root turnover rate (per year; Table S1). The turnover rates of fine roots were measured with a minirhizotron or by using reference values reported in the literature (Law et al., 2004; Wirth et al., 2002).

2.2. Models and Forcing Data Sets

This study included simulations from five DGVMs with two types of NPP allocation: functional balance and allometric relationships. The five DGVMs were the Lund-Potsdam-Jena dynamic global vegetation model (LPJ; Sitch et al., 2003), Land surface Processes and eXchanges (LPX-Bern 1.3; Spahni et al., 2013), Community Atmosphere Biosphere Land Exchange (CABLE 2.0; Wang et al., 2010), Integrated Biosphere Simulator (IBIS 2.1; Foley et al., 1996; Xia et al., 2015), and ORganizing Carbon and Hydrology in Dynamic EcosystEms (ORCHIDEE 1.9.6; Krinner et al., 2005). The LPJ and LPX-Bern 1.3 models adopt allometric relationships allocation schemes. The CABLE 2.0, IBIS 2.1, and ORCHIDEE 1.9.6 models incorporate functional balance allocation schemes. The NPP allocation algorithms of these five models are introduced briefly below.

2.2.1. Allometric Relationship Model

The LPJ model uses four allometric rules among biomass components to constrain the plant NPP allocation (Sitch et al., 2003). First, 10% of NPP is allocated to reproductive tissues (*afruit*). The remaining NPP is allocated to the leaves, sapwood, and fine roots by using an annual time step. The ratio of average individual LA (unit: m^2) to SA (unit: m^2) is constant ($K_{\text{la:sa}} = 8{,}000$).

$$\text{LA} = K_{\text{la:sa}} \times \text{SA} \tag{1}$$

The ratio of leaf biomass (C_{leaf}) to root biomass (C_{root}) depends on a maximum leaf-to-root mass ratio ($\text{lr}_{\max} = 1$ for tree) and water stress factors (ω, range of 0–1):

$$C_{\text{leaf}} = lr_{\max} \times \omega \times C_{\text{root}} \tag{2}$$

The allometry rules among plant height (H), crown area (CA), and stem diameter (D) depend on allometric constants ($k_{\text{allom1}} = 100$, $k_{\text{allom2}} = 40$, $k_{\text{allom3}} = 0.5$, and $k_{\text{rp}} = 1.6$). CA is constrained not to exceed a maximum value of 15 m^2.

$$H = k_{\text{allom2}} D^{k_{\text{allom3}}} \tag{3}$$

$$\text{CA} = k_{\text{allom1}} D^{k_{\text{rp}}} \tag{4}$$

In years of heat and/or water stress, NPP may not allow sufficient allocation to the leaves to allow full utilization of the current sapwood (given the constraint implied by equation (1)). This year's NPP is then

allocated to leaves and roots only, and the excess sapwood mass is transferred to the nonliving heartwood pool. In a drought year, there may be insufficient NPP to maintain current sapwood and leaf mass. Then, allocation is to fine roots only, and excess sapwood and leaf mass are transferred to the heartwood and litter pools.

The LPX-Bern 1.3 model (Keel et al., 2016; Keller et al., 2017; Spahni et al., 2013; Stocker et al., 2013) was developed from LPJ model. The LPX-Bern model uses the same annual allocation scheme and allometric equations as LPJ model. The differences in NPP allocation between LPX-Bern and LPJ models arise from differences in simulated soil water availability (equation (2)) and C pools (equations (1)-(4)). The NPP allocation and C pools affect each other through the four allometric equations (equations (1)–(4)). The advanced nitrogen limitation and updated model parameters in the LPX-Bern model change the NPP allocation by affecting the C pools (Keller et al., 2017).

For both LPJ and LPX-Bern models, *aleaf*, *awood*, and *aroot* were calculated as the ratios of annual net increases of leaf mass (*leafc_inc*), sapwood mass (*sapc_inc*), and fine root mass (*rootc_inc*) to the annual net increase in biomass (*bioc_inc*, excluding exudates and 10% allocated to reproduction from NPP), respectively.

$$\text{aleaf} = \text{leafc\_inc}/\text{bioc\_inc} \tag{5}$$

$$\text{awood} = \text{sapc\_inc}/\text{bioc\_inc} \tag{6}$$

$$\text{aroot} = \text{rootc\_inc}/\text{bioc\_inc} \tag{7}$$

2.2.2. Functional Balance Model

The CABLE 2.0 (Wang et al., 2010), IBIS 2.1 (Xia et al., 2015) and ORCHIDEE 1.9.6 models (Krinner et al., 2005) use the functional balance model proposed by Friedlingstein et al. (1999). For woody biomes, *aroot*, *awood*, and *aleaf* are expressed as follows:

$$\text{aroot} = 3r_0 \frac{L}{L + 2\min(W, N)} \tag{8}$$

$$\text{awood} = 3s_0 \frac{\min(W, N)}{2L + \min(W, N)} \tag{9}$$

$$\text{aleaf} = 1 - \text{awood} - \text{aroot} \tag{10}$$

where $\min(W,N)$ is the minimum availability of water (W) and nitrogen (N), and $r_0 = s_0 = 0.3$ in CABLE and ORCHIDEE; r_0 and s_0 are PFT-specific constants in IBIS (Xia et al., 2015). Light, water, and nitrogen availability and *aroot*, *awood*, and *aleaf* have no units and vary from 0 to 1.

Light availability (L) in CABLE and ORCHIDEE is calculated by the leaf area index (LAI; equation (11)). IBIS uses the cloud cover fraction (cld) to calculate light availability (L_{IBIS}; equation (12)).

$$L = \min\left[\max\left(e^{-0.5\text{LAI}}, l_{\min}\right), 1\right] \tag{11}$$

$$L_{\text{IBIS}} = 1 - \text{cld} \tag{12}$$

Water availability (W) in CABLE and IBIS is calculated by

$$W = \min\left[\max\left(\sum_{i=1}^{n} fr_i \frac{S_{\text{wi}} - S_{\text{wilt}}}{S_{\text{field}} - S_{\text{wi}}}, 0\right), 1\right] \tag{13}$$

where fr_i is the fraction of roots present in the ith ($n = 6$) soil layer, S_{wi} is the volumetric soil moisture content in the ith soil layer, and S_{field} and S_{wilt} represent the field capacity soil moisture content and the wilting point, respectively.

Water availability in ORCHIDEE (W_{ORC}) is calculated by assuming an exponential root profile decreasing with soil depth:

$$W_{ORC} = \max\left(\frac{\sum_{i=1}^{n} H_i e^{-z_i/\varsigma\Delta_i}}{\sum_{i=1}^{n} e^{-z_i/\varsigma\Delta_i}}, 0.1\right) \tag{14}$$

where H_i is the relative soil humidity at the ith soil layer and z_i and Δ_i are the depth and thickness of this layer, respectively. The root density profile is prescribed by $\zeta = 1.5$ m for trees.

Nitrogen availability (N) is calculated by combining the temperature (T_s) and moisture (W_s) limitations (Friedlingstein et al., 1999), where the T_s is calculated on the basis of a standard Q_{10} equation (Potter et al., 1993), and W_s is calculated as follows:

$$N = T_s \times W_s \tag{15}$$

$$T_s = Q_{10}^{\left(\frac{\sum_{i=1}^{n} f_{ri}T_{soili} - T_0}{10}\right)} \tag{16}$$

where T_{soili} is the temperature of the ith soil layer (°C) and $Q_{10} = 2.0$. T_0 is 30 °C for CABLE and IBIS, and 25 °C for ORCHIDEE. The W_s in ORCHIDEE is calculated in the same way as described in equation (14), with a depth constant of $\zeta = 0.2$ m.

ORCHIDEE allocates C to six compartments: leaves ($aroot_{ORC}$), aboveground ($asapab_{ORC}$), and belowground ($asapbe_{ORC}$) sapwood ($awood_{ORC} = asapab_{ORC} + asapbe_{ORC}$), fine roots ($aroot_{ORC}$), fruits ($afruit_{ORC}$), and the carbohydrate reserve ($areserve_{ORC}$).

$$afruit_{ORC} = 0.1 \tag{17}$$

$$areserve_{ORC} = (1-C) \times (1-afruit_{ORC}) \tag{18}$$

$$C = \frac{1}{1 + a(aleaf + aroot)} \tag{19}$$

where a is a tuning parameter ($a = 1$ for seasonal plants and $a = 0$ for evergreen trees). Consequently, evergreen trees have no carbohydrate reserve in the model. The allocation fractions of C among wood, leaf, and fine roots were calculated as

$$awood_{ORC} = awood \times (1-afruit_{ORC}) \times C \tag{20}$$

$$aleaf_{ORC} = aleaf \times (1-afruit_{ORC}) \times C \tag{21}$$

$$aroot_{ORC} = aroot \times (1-afruit_{ORC}) \times C \tag{22}$$

To compare the simulated NPP allocation ratios with our observations, we recalculated the NPP allocation fraction of wood, leaves, and fine roots by using $aleaf_{ORC}$, $aroot_{ORC}$, and $awood_{ORC}$ with the sum of $aleaf_{ORC}$, $awood_{ORC}$, $aroot_{ORC}$, and $areserve_{ORC}$ after excluding 10% allocated to fruits from the NPP. For deciduous trees, in addition to exclusion of fruits, the carbohydrate reserve was allocated to leaves and roots at the beginning of the growing season (2/3 to leaves and 1/3 to roots).

2.2.3. Forcing Data Sets

CRUNCEP version 7 meteorological 6-hourly forcing data set at 0.5° × 0.5° resolution and Climatic Research Unit Timeseries (CRU TS) 3.24 0.5° × 0.5° monthly climatology were used in this study. CRUNCEP is a combination of the CRU TS 3.24 0.5° × 0.5° monthly climatology covering the period 1901–2015 (Mitchell & Jones, 2005) and the 6-hourly National Centers for Environmental Prediction (NCEP) reanalysis 2.5° × 2.5° climatology, covering the period 1948–2015 (Kalnay et al., 1996). CABLE and ORCHIDEE models are forced by seven 6-hourly meteorological variables: the near surface air temperature (Tair), precipitation (Prec), incident shortwave radiation (Swd), incident longwave radiation (Lwd), specific humidity (Qair), wind speed (Ws), and pressure (Ps). IBIS model is forced by daily mean maximum and minimum temperatures, precipitation, relative humidity, wind speed, and cloud cover. The daily relative humidity is calculated

from Ps, Qair, and Tair (available at http://www.cactus2000.de/js/calchum.pdf). The LPJ model is forced by daily temperature, precipitation, and cloud cover. LPX-Bern model is forced by monthly temperature, precipitation, cloud cover, and wet days, calculated from CRUNCEP or derived from CRU TS. The annual mean global surface CO_2 concentration for 1901–2015 is a combination of ice-core records from the Antarctic for 1901–1958 (Etheridge et al., 1996) and atmospheric observations since 1959 (Keeling & Whorf, 2005; available at https://www.esrl.noaa.gov/gmd/ccgg/trends/data.html).

2.3. Simulation Protocol

Five terrestrial carbon cycle models were run at all study sites. The model simulation included two periods: spin-up and transient simulations. To obtain the initial sizes of the terrestrial ecosystem C pools, we spun the model by recycling climate data for 1901–1930 and an atmospheric CO_2 concentration of 297.0 ppm (i.e., the 1901 level). The spin up time of the CABLE, IBIS, LPJ, and ORCHIDEE models is 1,000 years. LPX-Bern model uses a 1,500-year spin up. We then set all plant carbon pools to zero and the LAI to a minimum value (0.01) while maintaining the steady state values of all litter and soil carbon pools and ran the transient simulation to study how NPP allocation varies with stand age. For the transient simulations, the models were driven from the year of establishment to 2015 under forcing with varying climate and atmospheric CO_2 concentrations if the seedlings were established after 1901. The year of seedling establishment (Yr_{ets}) at each site was estimated with the year of observation (Yr_{obs}) and forest stand age ($Yr_{ets} = Yr_{obs}$-age + 1). If the seedlings were established before 1901, we ran the model by recycling the climate data for 1901–1930 and an atmospheric CO_2 concentration of 297.0 ppm until the year 1901. The transient simulations of five models were used to compare with observations at the same stand age. The terrestrial ecosystem models used the concept of PFT to describe vegetation distributions. The different PFTs were distinguished by specific biogeochemical parameters. In this study, the PFT of each site was simulated according to the observed vegetation type (Table S1).

3. Results

3.1. Observed Spatial Patterns of NPP Allocation

The NPP allocation among plant components showed substantial geographical heterogeneity. For analysis of the spatial patterns of NPP allocation among the three plant C pools, we considered only old forests to eliminate the effects of forest stand age on NPP allocation. For boreal and temperate forests, old forests refer to stands with an age > 100 years. For tropical forests, stand age was not quantified in most studies; only sites described as "primary" old-growth forests were included in this study. Among all mature forests (61 site-years of observations at 44 sites), *aleaf* increased with increasing mean annual temperature (*MAT*) in all sites (Figure 2a); notably, a significantly increased trend was observed over boreal and temperature forests ($y = 0.79x + 18.28$, $R^2 = 0.37$, $p < 0.05$) but not over tropical forest ($y = -0.30x + 43.41$, $R^2 = 0.02$, $p = 0.35$). In contrast, *aroot* significantly decreased with *MAT* in all sites (Figure 2c). The *aleaf* and *aroot* showed opposite changes with increasing annual precipitation (*AP*; Figures 2d and 2f). When *AP* was <2,000 mm, *aleaf* and *aroot* increased and decreased with increasing *AP*, respectively (Figures 2d and 2f); with a further increase in *AP*, corresponding decreases and increases were observed. We did not detect a significant relationship between *awood* and *MAT* or *AP* across all sites (Figures 2b and 2e). However, for old-growth tropical forest, *awood* increased with increasing *AP* (Figure 2e).

The NPP allocations among plant components varied with stand age. Because the stand age of tropical forests is very difficult to determine, the relationships between NPP allocations and stand age were examined only for temperate and boreal forests (70 site-years). For those two types of forests, *aleaf* and *awood* were negatively correlated with stand age (Figures 3a and 3b), but *aroot* was positively correlated with stand age (Figure 3c). Similar change trends were also found for the temperate and boreal forests. However, the negative correlation between *aleaf* and stand age in temperate forests was not significant. For boreal forests, *awood* and stand age also showed no significant negative correlation.

The observations showed substantial differences in allocation ratios among different ecosystem types (Figure 4). The tropical broadleaf evergreen forests showed the largest *aleaf* among all vegetation types (Figure 4b). The largest *awood* was for temperate forests, and the largest *aroot* was for boreal forests (Figure 4). Notably, the old-growth forests in cold climate zones (e.g., boreal needleleaf evergreen) had
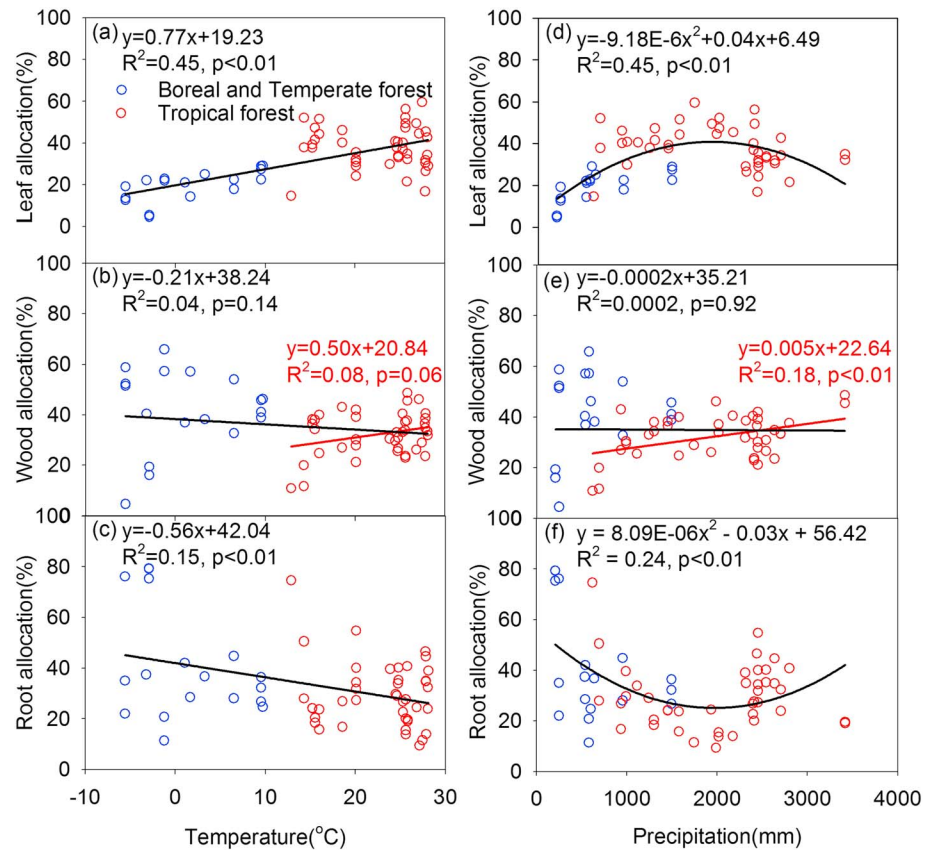
Figure 2. Changes in the allocation ratios of leaves, wood, and fine roots with (a–c) mean annual temperature and (d–f) precipitation at old-growth sites for tropical, temperate, and boreal forests (61 site-years). The black lines are the fitting lines between the observed allocation ratios and temperature and precipitation over boreal, temperature, and tropical forests. The red lines are the fitting lines between the observed allocation ratios and temperature and precipitation over tropical forests.

higher $aroot$ than warm and humid tropical forests (Figure 4b). In addition, the $awood$ was larger for young stands than for mature stands across all forest types, especially for temperate needleleaf evergreen (Figure 4).

3.2. Model-Data Comparisons

All five models performed poorly in capturing the spatial patterns of $awood$, $aleaf$ and $aroot$. No correlations were found between the simulated and observed NPP allocation ratios in the three plant pools (112 site-years; Figure 5). For mature forests, all five models captured the observed decreasing trend in NPP allocation to fine roots, with an increase in MAT (Figure 6c). For $AP < 2,000$ mm, all five models reproduced the decreasing trend in $aroot$ with increasing AP (Figure 6f). The five models did not simulate the increasing trend in $aroot$ with further increases in AP. However, the simulated $aleaf$ showed decreasing or constant values with AP and MAT, but an increasing trend for $awood$, contrary to the observations (Figures 6a, 6b, 6d, and 6e).

The observations showed that $awood$ and $aleaf$ negatively correlated with $aroot$, and the correlation between $awood$ and $aleaf$ was not significant (Figures 7a–7c). All five models successfully reproduced the negative correlations between $awood$ and $aroot$ (Figures 7d, 7g, 7j, 7m, and 7p) but simulated a positive correlation between $aleaf$ and $aroot$ (Figures 7h, 7k, 7n, and 7q) and a negative correlation between $awood$ and $aleaf$ (Figures 7f, 7i, 7l, 7o, and 7r). Therefore, none of the five models captured the negative correlation between $aleaf$ and $aroot$.

None of the models reproduced the observed relationships between all three allocation ratios and stand age. Over all of the boreal and temperate forest sites, the observed $awood$ and $aroot$ decreased and increased with stand age, respectively (Figure 3). Only ORCHIDEE model reproduced the general trends in $awood$ and
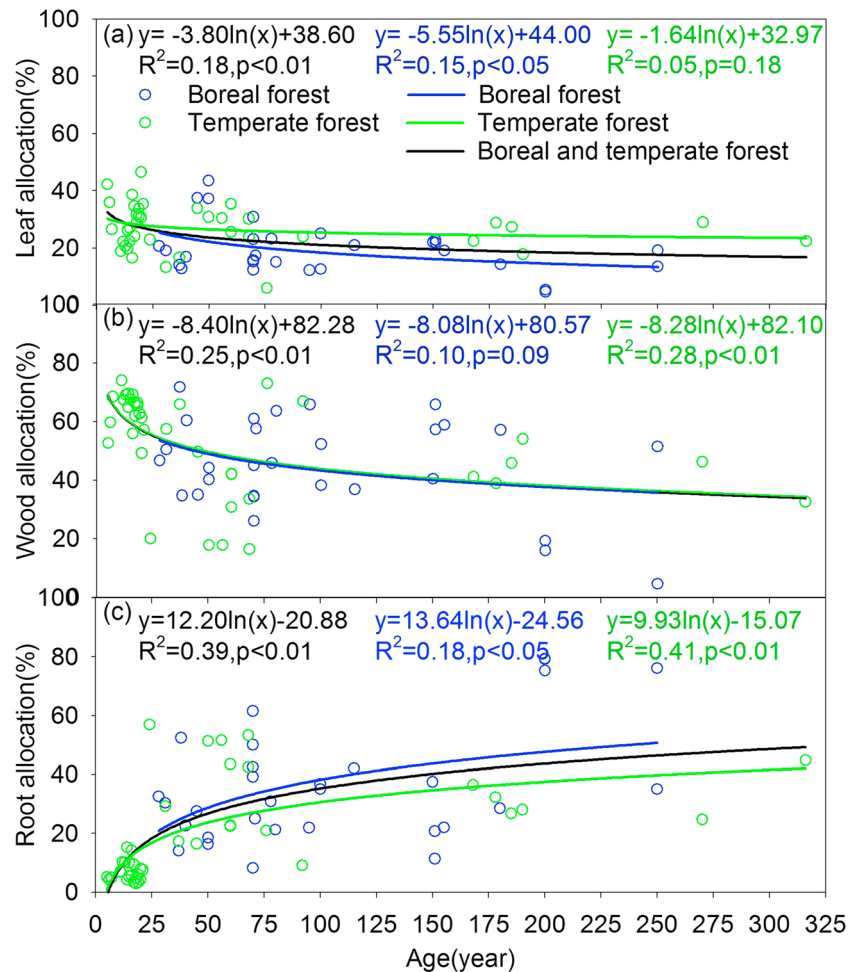
Figure 3. Changes in the net primary production allocation ratios of (a) leaves, (b) wood, and (c) fine roots with stand age for boreal and temperate forest sites (70 site-years).

$aroot$ with stand age; however, the observations showed large differences in magnitude (Figures 8b and 8c). LPX-Bern model captured the decreased $aleaf$ with stand age (Figure 8a). CABLE and ORCHIDEE models simulated an increased $aleaf$ with stand age (Figure 8a) that was opposite from the observed trends.

4. Discussion

4.1. Spatial Patterns in NPP Allocation

The data that we compiled for forest sites indicated decreasing $aroot$ with increasing MAT and AP (for $AP <$ 2,000 mm; Figures 2c and 2f). Previous studies have reported that $aroot$ increases with decreasing nitrogen and water availability in various forests (Aber et al., 1985; Gower et al., 1992; Jiménez et al., 2009; Portsmuth & Niinemets, 2007; Tilman, 1988). Our results support the conclusion that plants tend to allocate more C to roots in dry regions where water is the most important limiting resource (Coomes & Grubb, 2000; Devakumar et al., 1999; Reynolds & Pacala, 1993; Santantonio, 1989; Vogt et al., 1987). In addition, soil nitrogen and phosphorus mineralization is a crucial process regulating the availability of nutrients for plant growth; high temperatures and more water would increase such mineralization (Chapin et al., 2011). A meta-analysis has indicated that nitrogen mineralization is negatively correlated with increasing latitude (Liu et al., 2017), in agreement with a higher $aroot$ with lower MAT and AP (Figures 2c and 2f).

In addition, biological factors, for example, forest stand development, are other strong regulators of NPP allocation among plant components. Our results are consistent with those from previous studies
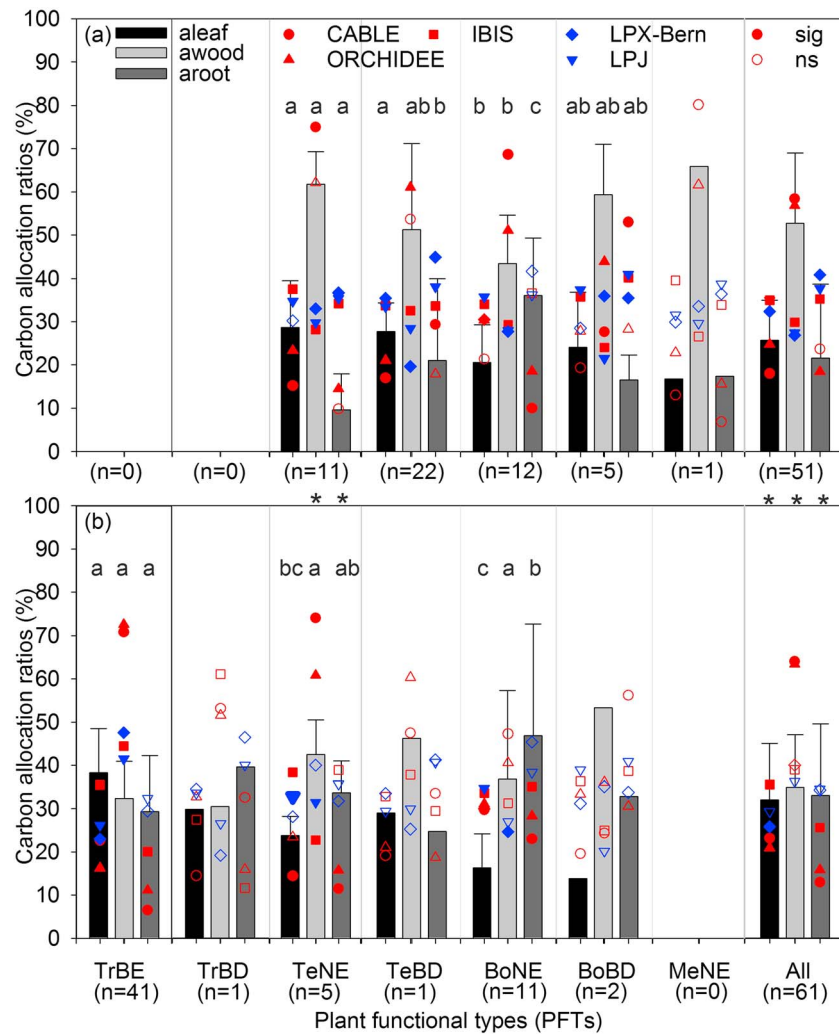
Figure 4. Comparison of the net primary production allocation ratios of leaves (*aleaf*), wood (*awood*), and fine roots (*aroot*) for the various forest types. (a) Young stands (stand age <100 years) and (b) old-growth (mature) stands (stand age >100 years). The letters (e.g., a, b, c, ab in panel a and a, b, c, ab, bc in panel b) above the error bars indicate the significance of the differences in observational net primary production (NPP) allocation ratios among forest types. The red circles, squares, and upward-pointing triangles refer to the NPP allocation ratios of Community Atmosphere Biosphere Land Exchange (CABLE), Integrated Biosphere Simulator (IBIS), and ORganizing Carbon and Hydrology in Dynamic EcosystEms (ORCHIDEE) models, respectively (functional balance model). The blue downward-pointing triangles and diamonds refer to the simulated NPP allocation from the Lund-Potsdam-Jena (LPJ) and Land surface Processes and eXchanges (LPX)-Bern models, respectively (allometric relationship models). The solid and hollow shapes indicate significant ("sig") and nonsignificant ("ns") differences in the simulated allocation ratios and observational estimates (i.e., "sig" and "ns" in panel a). "n" at the bottom of panels indicates the number of observations. The asterisks between panels (a) and (b) indicate significant differences in allocation ratios between young and mature stands. TrBE: tropical broadleaf evergreen forest; TrBD: tropical broadleaf deciduous forest; TeNE: temperate needleleaf evergreen forest; TeBD: temperate broadleaf deciduous forest; BoNE: boreal needleleaf evergreen forest; BoBD: boreal broadleaf deciduous forest; MeNE: Mediterranean needleleaf evergreen forest.

suggesting that wood production at the stand level increases in early stages of stand development, and *awood* then declines over a period of years to centuries (Figure 3b; Gower et al., 1996; Ryan et al., 1997; Genet et al., 2010). In addition, our results showed that *aroot* increased at the expense of *awood* as stands became older (Figures 3b and 3c). Several processes can explain this age-related trend for wood and fine roots. The height-related hydraulic resistance for old stands is considered one of the most important causes of decreased wood allocation. Increases in tree height are associated with increases in the hydraulic resistance of xylem, which may lead to decreases in the turgor of living cells and have potentially negative consequences on cambial
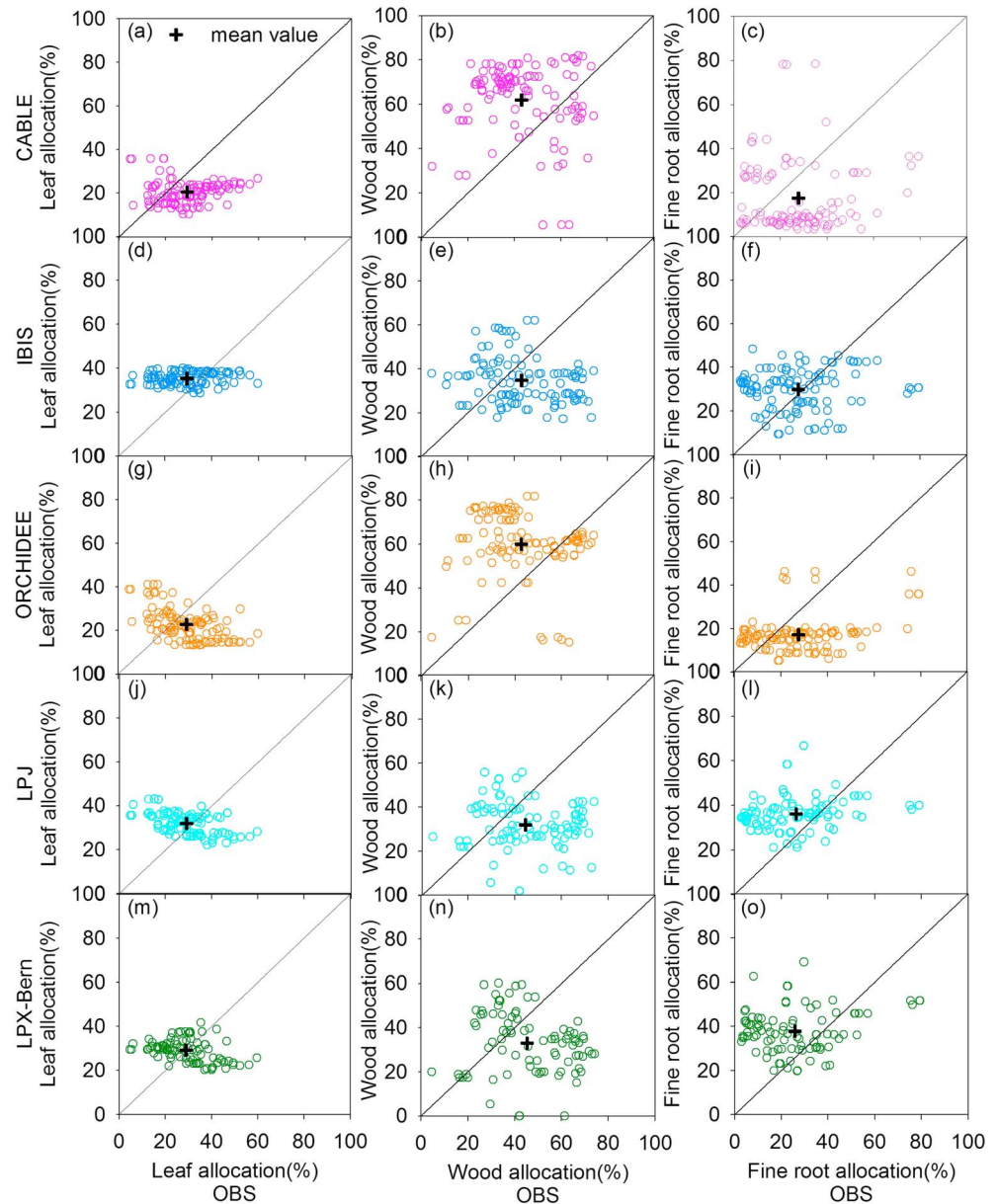
Figure 5. Correlations between simulated and observed (OBS) allocation ratios for leaves, wood and fine roots at all sites (112 site-years). The solid lines are 1:1 correspondence lines. The black crosses indicate the mean values of simulated and observed net primary production allocation ratios.

activity (Woodruff et al., 2004). This constraint may result in a height-related sink limitation of growth (Woodruff & Meinzer, 2011a, 2011b). In addition, the increased competition for soil water and nutrients would result in proportionally greater belowground C flux in mature stands. This conclusion is based on previous fertilization/irrigation experiments showing that increased availability of belowground resources can cause a shift in NPP allocation from belowground to aboveground (Gower et al., 1992, 1994; Haynes & Gower, 1995; Keith et al., 1997). Some evidence suggests that the nitrogen content in foliage and roots decreases with stand age, and inorganic soil nitrogen availability decreases in mature stands (Litton et al., 2004). Therefore, more C is allocated to fine roots with decreasing nitrogen resources.

The components of NPP in this study were measured or estimated through different methods, thus resulting in some uncertainty in the observed patterns of NPP allocation. Leaf NPP is measured by collecting abscised leaves with the highest reliability (Norby et al., 2002). The aboveground wood NPP is estimated from the
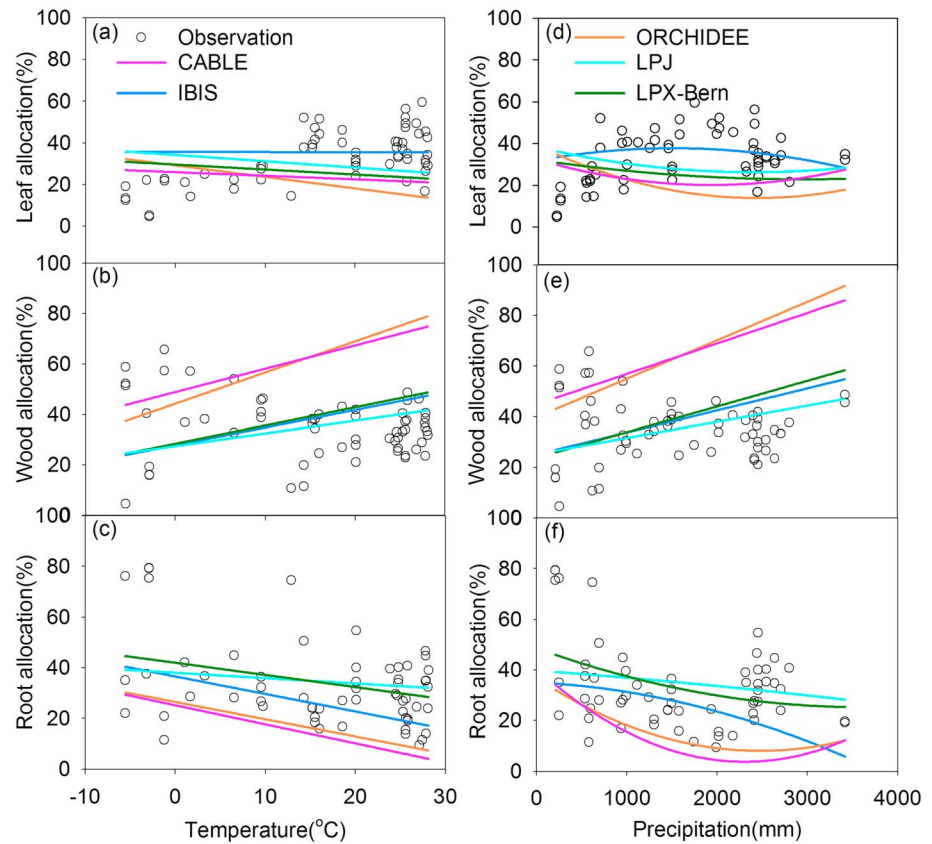
Figure 6. Changes in the allocation ratios of foliage, wood and fine roots with mean annual temperature (a–c) and precipitation (d–f) for each of the five models at old forest sites (61 site-years). The cycles represent the observed net primary production allocation ratios. The five lines refer to the regression lines between the simulated net primary production allocation ratios and climate variables.

wood biomass increase. Stand-level allometric functions are used to estimate aboveground wood biomass from the stem diameter at breast height, tree height, and wood density (Chave et al., 2005; Wirth et al., 2002). At 86% of the sites, coarse root NPP was estimated with allometric equations (Table S1). The uncertainty in wood NPP is mainly from the allometric equation used to estimate biomass. The fine root NPP was estimated through the most common methods, such as minirhizotron, soil core, and ingrowth core. These methods may underestimate fine root NPP, owing to fine root herbivory or the turnover of fine roots faster than the interval at which they are measured (Malhi et al., 2011).

4.2. Model Performance

In this study, we sought to examine the performance of model representation of NPP allocation through a model-data comparison. It is important to verify whether the NPP allocation in fast (foliage and fine roots) and slow (wood) pools is represented equally well by models across space and forest succession, because this representation is particularly relevant to understanding the effects of climate and increasing atmospheric CO_2 concentration, and afforestation, deforestation, or other types of disturbance altering the function and age structure of forests. Model performance depends strongly on model algorithms and on the representation of the major processes controlling environmental and biological regulation of NPP allocation.

None of the model simulations in this study matched well with the observed NPP allocation among the three plant components for all vegetation types. The models did not correctly simulate the averaged patterns of NPP allocation (Figure 5). Poor model performance of NPP allocation largely results from inappropriate parameterization. Most NPP allocation models are parameterized by using biomass observations over regional or global scales (Bloom et al., 2016; Xia et al., 2015). However, uncertainties in biomass turnover strongly affect estimates of the NPP allocation ratio. Previous studies have suggested large uncertainties in biomass
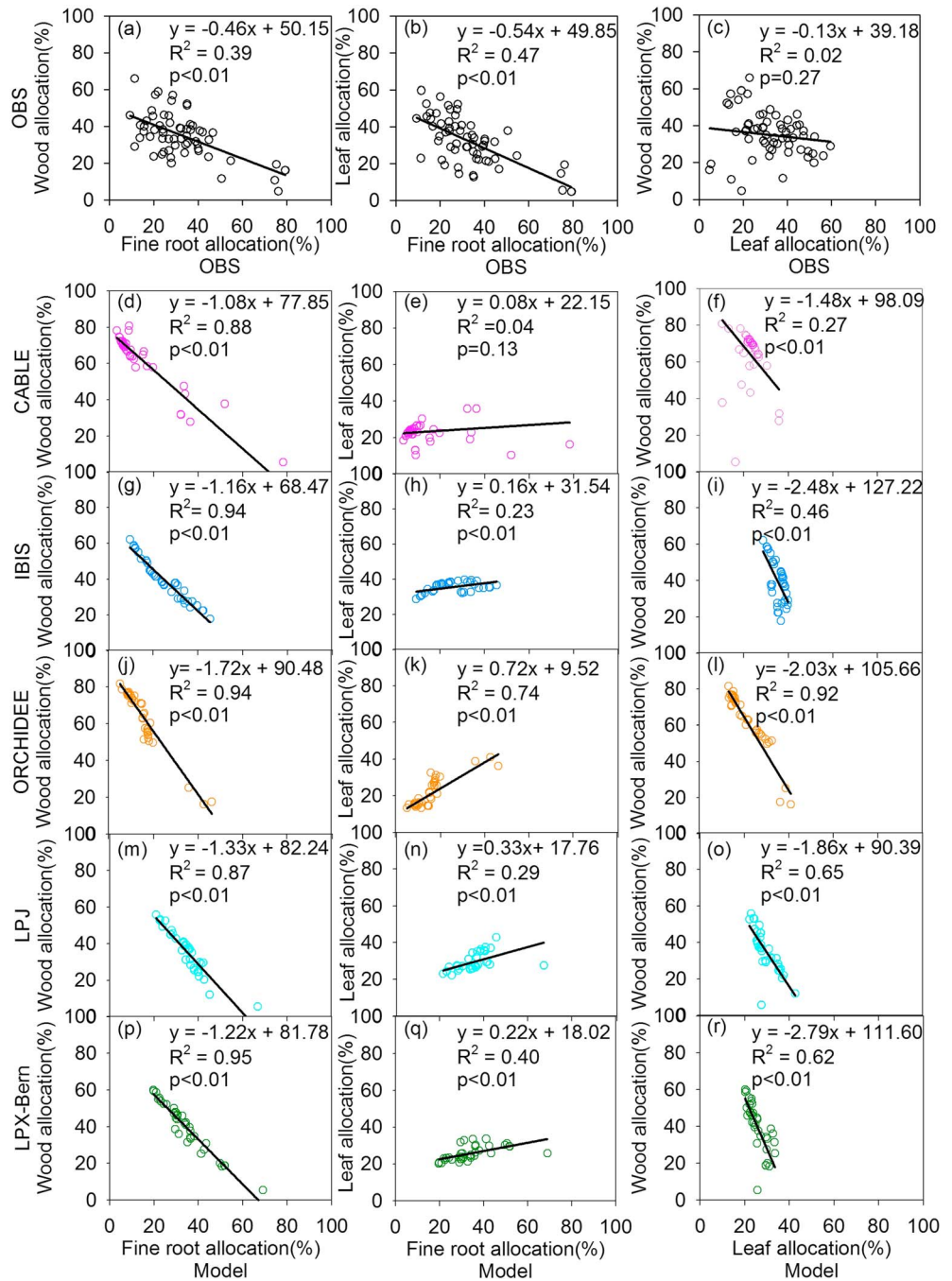
Figure 7. The relationships of allocation ratios among leaves, wood and fine roots at old-growth forest sites (61 site-years) for (a–c) observational (OBS) estimates and (d–r) each of the five models.

turnover time in the current land biosphere models (Carvalhais et al., 2014; Friend et al., 2014). For example, Zhang et al. (2016) have reported that the default leaf longevity in LPJ differs from observations for four major forest types—notably, the observed leaf longevity of boreal needleleaf forest (6.5 years) was found to be more than three times the default value (2 years). Because both allocation and turnover time govern C stocks and sequestration potential, the parameterization of NPP allocation and of turnover time must be considered together by using the best available observations.

In this study, the five models did not adequately capture the spatial patterns in NPP allocation with climate (i.e., MAT and AP) and stand age, thus implying large uncertainties in model structure and parameter
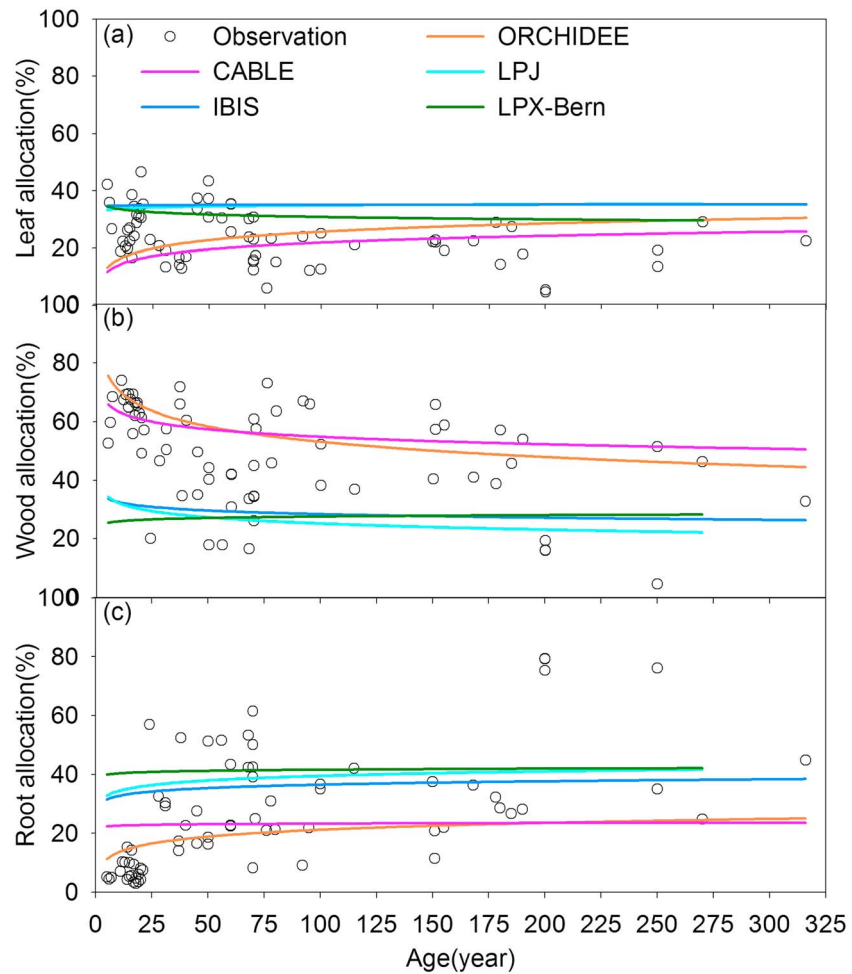
Figure 8. Changes in the allocation ratios of (a) leaves, (b) wood, and (c) fine roots with stand age for each of the five models, for boreal and temperate forest sites (70 site-years). The fit lines of the Lund-Potsdam-Jena (LPJ) and Land surface Processes and eXchanges (LPX)-Bern models are shorter than those of the other three models because the observed plant functional type could not occur under the climatic conditions of several sites. Therefore, the data sizes of LPJ and LPX-Bern models are slightly lower than those of the other three models.

values. All five models approximately reproduced the decreased a_{root} with increasing AP and MAT, but the simulated results were opposite from the observed spatial gradients of a_{wood} and a_{leaf} (Figures 2 and 6). Functional balance models simulate a_{root} and a_{wood} according to environmental regulation (Xia et al., 2015), and a_{leaf} is the residual of a_{wood} and a_{root}. Ecological studies do not support the concept of prioritization of photosynthetic products, because all component fluxes have been reported to rise with increased NPP in observations at 57 sites (Litton et al., 2007); these results do not confirm the assumption that the highest-priority pool fills first, followed by the next priority. This study found variations in a_{leaf} with climatic and biological variables, thus indicating that NPP tends to be allocated to foliage as the highest priority. Therefore, our results suggest that the current functional balance models do not set the priority correctly, thereby partly explaining why the simulated correlations of a_{root} and a_{leaf} contrasted with the observed correlations (Figures 7h and 7k). Future NPP allocation models must reexamine the relationships of NPP allocation with the environment.

The CABLE and ORCHIDEE models correctly simulated the increase in a_{wood} with stand age in the initial forest growth stage (Figure 9b). These two models simulate the light availability by using LAI. During early stand development, the LAI increases gradually, thus decreasing light availability and increasing a_{wood} to alleviate the light restriction, according to the principle of functional balance models (Friedlingstein et al., 1999). However, after approximately 8 to 10 years, the LAI can reach a large value because it is not
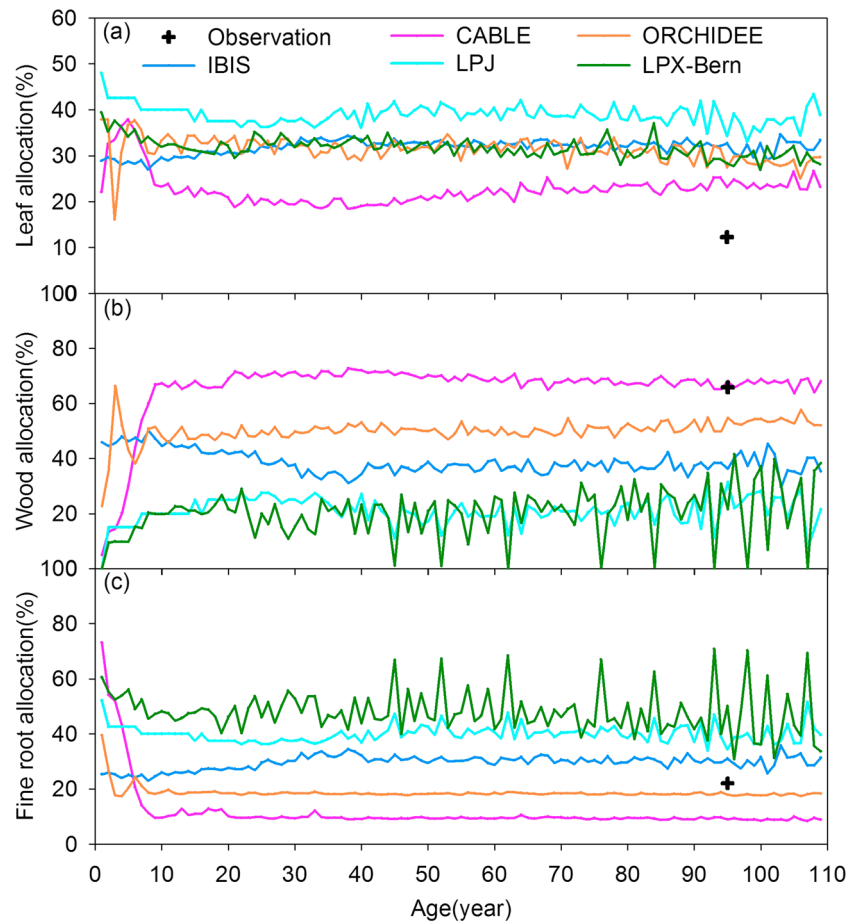
Figure 9. Simulated changes in the net primary production allocation ratios of (a) leaves, (b) wood, and (c) fine roots with stand age at Yenisey region. This boreal needleleaf evergreen forest stand was established in 1906 and observed in 2000 (i. e., age = 95 years). The black crosses indicate observed values.

parameterized to increase until canopy closure, and it then decreases with stand age, and the allocations of NPP will be determined by the water and nutrient availability (Xia et al., 2015). Therefore, these two models cannot represent the decrease in $awood$ and the increase in $aroot$ with higher stand age because they do not integrate the competition of plant communities for soil water and nutrients (Figures 3 and 8).

The LPJ and LPX-Bern models are also able to reproduce the increase in $awood$ in early phases of forest growth. However, by design, they do not capture the subsequent decrease in this fraction with stand age (Figure 9b). The LPJ and LPX-Bern models are based on an average individual approach to represent trees. Under constant environmental conditions, a climatological equilibrium for the fraction of NPP allocated to leaves, wood, and roots will be approached. The allocations within the LPJ and LPX-Bern models are controlled by allometric equations. During early stages of forest growth, such as after clearing, NPP is mainly represented in $aleaf$ and $aroot$ (Figures 9a and 9c). To maintain the fixed ratio between LA and SA (equation (1)), more C is allocated to sapwood with the increase in the leaf C pool, and SA (C pool) consequently increases quickly. The fraction of NPP going to $awood$ would decrease in these models only if NPP is insufficient to maintain the ratio between LA and SA, for example, in response to drought. If the NPP in a given year is very low, the biomass goes first to leaf and fine roots, and consequently, the sapwood allocation is set to 0 (Figure 9b).

Previous studies have suggested that the allometric relationship approach, based on allometric rules among biomass components, is relatively more successful at capturing the observed NPP allocation among plant components responding to elevated CO_2, one owing to constraints by biomass fractions (De Kauwe et al., 2014). Our comparisons implied similar performance for allometric relationship and functional balance

models in reproducing the allocation ratios (Figure 4) and changes in NPP allocation with climate gradients and stand age (Figures 6 and 8). Allometric relationship models poorly reproduce the spatial patterns in NPP allocation for the three plant components. Similarly, this family of models can simulate the changes in fine root ratios with precipitation, but they do not indicate spatial patterns in root and leaf ratios. Allometric relationship models have been developed by using observations of multiple sites and forest types (Shinozaki et al., 1964), and they essentially indicate the spatial characteristics of biomass allocation. However, these models are used to simulate temporal variations at a given site according to the principle of spatial sequence rather than a time successional sequence. Usually, allometric relationship models use fixed ratios among plant components. However, numerous studies have reported varying allometric relationships with different climates and stand ages (Albrektson, 1984; Berninger & Nikinmaa, 1997; Mencuccini & Grace, 1995). In addition, allometric relationship models aim at simulating biomass allocation. A comparison of land biosphere models for biomass has shown that models with relatively shorter wood turnover times generally yield results closer to observed allometries (Wolf et al., 2011). Our results indicate that the better allometric relationship models should adopt dynamic allometric ratios among plant components, which should be regulated by multiple resources (e.g., soil water and nutrients) and stand age.

4.3. Effects on C Storage Estimation

Numerous studies have reported substantial effects of NPP allocation on C cycle estimates (Friedlingstein et al., 1999; Malhi et al., 2011; Xia et al., 2017). Jones et al. (2013) have shown a large spread in the simulated change in the land C-store of approximately 250–400 Pg C by 2100 from a series of model simulations run as part of CMIP5—one important reason for this finding is the large differences NPP allocation and pool turnover among models. Models are generally spun up to reach equilibrium biomass to match the estimated global biomass (Olson et al., 1983; Saatchi et al., 2011). However, the errors derived from NPP allocation simulations are often counteracted by uncertainties in biomass turnover (Friend et al., 2014). Our study showed large differences between the simulated NPP allocation ratios of plant components and observational data, thus implying that biases in NPP allocation must be compensated for by biases in biomass turnover, if the models can reasonably simulate biomass. These models match the good biomass estimation through two incorrect intermediate processes (i.e., NPP allocation and biomass turnover), thus resulting in substantial simulation errors in future C budget projections.

Some models try to improve the turnover of plant components to better reproduce biomass (Xue et al., 2017). However, if the NPP allocation schemes in the current models were used, the global simulations would probably suffer from systematic errors. Our results show that all five models overestimate *aleaf* for cold and dry regions, but underestimate it for warm and moist regions (Figures 6a and 6d). If the uncertainties in turnover are not considered, the current models tend to overestimate foliage biomass for cold and dry regions.

Forests worldwide are far from equilibrium and in many cases are becoming demographically younger because of harvesting (Houghton, 2005), increasing fire frequency (Soja et al., 2007), enhanced mortality from climate or herbivory (Ayres & Lombardero, 2000; Van Mantgem et al., 2009) and woody plant encroachment (Asner et al., 2003; Mast et al., 1997). Thus, estimating the current and future C cycle arguably requires greater fidelity during early growth. The analysis above suggests that none of the land biosphere models can reproduce the changes in *aleaf*, *aroot*, and *awood* with stand age, especially the decreasing trend in *awood*. Wood production influences long-term C storage more than all other components of NPP, because of the durability of wood (Chambers et al., 2001). At the global scale, the rate of C storage via wood production currently exceeds the rate of losses via tree death, thus making forests an important C sink (Pan et al., 2011). The world's forests are recognized to help abate the rise in atmospheric CO_2. Consequently, understanding the drivers of stand-level wood production at a regional scale will be central to predicting changes in the global forest C sink over the coming century. However, the current models tend to overestimate wood production for old stands because of inappropriate NPP allocation schemes, and they overestimate the C sink of forest ecosystems.

4.4. Ways to Improve NPP Allocation Models

The results presented in this study may lead to better modeling of NPP allocation through two aspects. First, Figure 4 shows the observed NPP allocation values of both young and mature forests for various PFTs in the DGVMs. The high model-to-model variation in the simulated NPP allocation in Figure 4 is caused by the

different NPP allocation model hypotheses and parameters. The NPP allocation ratios to wood in CABLE and ORCHIDEE models are much higher than those of the other three models, mainly because the CABLE and ORCHIDEE models use LAI to calculate the light availability. As the LAI of forests increases, the light availability strongly decreases. When plants are under severe light stress, the NPP allocation to wood becomes very high. The way to improve the NPP allocation model is to use observed NPP allocation data to constrain the parameters or test new resource availability equations (e.g., the light availability equation) of the allocation models.

Second, this study shows the systematically poor performance of models on the age-dependent patterns of NPP allocation. Model limitations with regard to accurate representation of the forest structure and demographic processes deserve more attention in NPP allocation model development (Fatichi et al., 2019). Meanwhile, more physiological representation of age-related NPP allocation processes is needed in DGVMs. For example, the decrease in wood allocation, induced by height-related hydraulic resistance and the competition process for soil water and nutrients in mature forest stands, could be coupled and included in DGVMs (Ryan et al., 2004; Woodruff et al., 2004; Woodruff & Meinzer, 2011a, 2011b). The data collected in this study could be used to test those model hypotheses.

5. Conclusions

Using the observed NPP allocation data, this study explored the global patterns in NPP allocation regulated by environment and stand age and the performance of the allometric relationship and functional balance allocation models in five widely used DGVMs. Over all mature forests, allocation to fine roots decreased with increasing MAT and precipitation. There was a trade-off between allocation to leaves and fine roots. In addition, allocation to wood and leaves decreased significantly with stand age, and allocation to fine roots significantly increased with stand age. All five models approximately captured the trend of decreasing allocation to fine roots with increasing MAT and precipitation but did not capture changes in allocation to leaves and wood. There were substantial differences in the simulated NPP allocation ratios compared with observations over all forest types. None of the five models reproduced the decreased allocation to wood and increased allocation to fine roots with stand age. Overall, our comparisons implied similar performance between allometric relationship and functional balance models. Accurate understanding of the responses of NPP allocation to climate change and biological parameters is needed to improve future carbon budget projections.

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