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Canopy photosynthetic capacity drives contrasting age dynamics of resource use efficiencies between mature temperate evergreen and deciduous forests

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Abstract

Forest resource use efficiencies (RUEs) can vary with tree age, but the nature of these trends and their underlying mechanisms are not well understood. Understanding the age dynamics of forest RUEs and their drivers is vital for assessing the trade-offs between forest functions and resource consumption, making rational management policy, and projecting ecosystem carbon dynamics. Here we used the FLUXNET2015 and AmeriFlux datasets and published literature to explore the age-dependent variability of forest light use efficiency (LUE) and inherent water use efficiency as well as their main regulatory variables in temperate regions. Our results showed that evergreen forest RUEs initially increased before reaching the mature stage (i.e., around 90 years old), and then gradually declined; in contrast, RUEs continuously increased with age for mature deciduous forests. Changing canopy photosynthetic capacity (A_{max}) was the primary cause of age-related changes in RUEs across temperate forest sites. More importantly, soil nitrogen (N) increased in mature deciduous forests through time but decreased in older evergreen forests. The age-dependent changes in soil N were closely linked with the age dynamics of A_{max} for mature temperate forests. Additionally, soil nutrient conditions played a greater role in deciduous forest RUEs than evergreen forest RUEs. This study highlights the importance of stand age and forest type on temperate forest RUEs over the long term.

KEYWORDS

age pattern, eddy covariance, light use efficiency, maximum photosynthetic capacity, soil nitrogen, temperate forests, water use efficiency

1 | INTRODUCTION

Temperate forests play an important role in regulating the global carbon cycle (Forkel et al., 2016; Pan et al., 2011), mitigating global warming (IPCC, 2013), and contributing to bioenergy production (Hudiburg, Law, Wirth, & Luyssaert, 2011). However, the spatial and temporal variability of these ecosystem functions and services can vary as a function of age (Amiro et al., 2010; Luyssaert et al., 2008; Tang, Luyssaert, Richardson, Kutsch, & Janssens, 2014). As large areas of temperate forests are growing older (Curtis & Gough, 2018; Tian et al., 2015), it is imperative to understand age-related linkages between forest functions and resource utilization. Few mechanistic models distinguish between young and mature forests when assessing their roles in the terrestrial carbon cycle or their responses to global climate change (Marthews et al., 2012; Niinemets, Tenhunen, & Beyschlag, 2004; Peng et al., 2014). Moreover, some site-level syntheses and meta-analysis studies have ignored the substantial differences in forest age (Garbulsky et al., 2010; Lu et al., 2017; Saurer et al., 2014), which increases uncertainty in quantifying forest functions at the regional or global scale.

Resource use efficiency (RUE) is generally defined as the amount of carbon obtained per unit of a resource consumed. At the ecosystem scale, light use efficiency (LUE; i.e., the capacity of an ecosystem to use solar radiation for photosynthesis) and water use efficiency (i.e., the trade-off between photosynthetic productivity and water consumption) are essential characteristics reflecting ecosystem functions and adaptability to climate change (Keenan et al., 2013; Xu et al., 2020). It is well recognized that forest growth increases with age during early stages of development but often declines after reaching a peak (Besnard et al., 2018; Luyssaert et al., 2008; Tang et al., 2014). As young trees grow, biomass accumulation and canopy development follow a pattern that stems from the optimization of investments required to access more light and water. There is a prevailing view that the marginal return of carbon gain per unit of resource used decreases as the supply of a resource (e.g., light or water) increases (Binkley, Stape, & Ryan, 2004; Niu et al., 2011; Pastor & Bridgham, 1999), which likely leads to mismatched age patterns between forest RUEs and tree growth. Additionally, trees can regulate trade-offs between resources, enhancing the use efficiency of a scarce resource while lowering the efficiency of an abundant resource, at least over the short term (Hidaka & Kitayama, 2009; Tarvainen, Räntfors, & Wallin, 2015). This mechanism may result in divergent age trends of RUEs. Accordingly, two vital questions emerge: (a) Are the age patterns of forest RUEs similar to that of tree growth? (b) Are the RUEs strongly coupled across chronosequences?

Many studies have reported that forest RUEs are mainly regulated by climate variables (e.g., temperature and precipitation; Huang et al., 2016; Linares & Camarero, 2012; Liu et al., 2019), whereas some recent studies found that RUEs depend more heavily on nutrient availability and stand age at the decadal scale (Li, Tian, Yang, & Niu, 2018; Musavi et al., 2017; Zhang, Huang, Zhang, Zhu, & Di, 2019). Specifically, forest RUEs are highly sensitive to soil or leaf nutrient conditions (LeBauer & Treseder, 2008; Vicca et al., 2012) and age-related biological characteristics, such as canopy photosynthetic capacity (A_{max}; Drake, Raetz, Davis, & Delucia, 2010; Ollinger et al., 2008) and leaf area index (LAI; le Maire et al., 2013; McMillan & Goulden, 2008). In addition, forest management practices prevailing in temperate forests may initiate a cascade of structural and nutrient changes that shift resource allocation and resource availability, increasing the uncertainties in the variation of temperate forest RUEs with age (Curtis & Gough, 2018). However, the dominant factor regulating the age dynamics of forest RUEs remains unclear. Moreover, forest canopy features and tree physiological functions vary at different age stages (Drake, Davis, Raetz, & Delucia, 2011; Steppe, Niinemets, & Teskey, 2011), which may cause the relative importance of different causal factors to change over time. Consequently, exploring how these biophysical drivers mediate forest RUEs as a function of age is essential for elucidating the underlying mechanisms and modeling forest ecosystem processes over time.

Although there is a consensus that forest RUEs increase before canopy closure, the age-related dynamics of mature forest RUEs and regulatory mechanisms are still debatable (Binkley et al., 2004; Fernández & Gyenge, 2009). Many studies have reported that hydraulic limitations increasingly induce stomatal closure with tree aging, decreasing photosynthesis and RUE (Drake et al., 2010; Ryan, Phillips, & Bond, 2006). Hydraulic limitation increases with the overall water conduction path length (e.g., tree height and branch length; Baret, Pepin, & Pothier, 2018; Delzon & Loustau, 2005; Ryan et al., 2006). However, hydraulic structures (e.g., cavitation resistance and sapwood conductivity) related to tree height and age-related genetic expression play an opposite role by offsetting the hydraulic limitation (Niinemets, 2002; Thomas & Winner, 2002). Other studies have suggested that soil nitrogen (N) could modulate the variation of mature forest A_{max} and RUEs (Fernández & Gyenge, 2009; Menge, Hedin, & Pacala, 2012). Although soil N or leaf N is tightly related to ecosystem photosynthetic rate and productivity in various forest types (Elser et al., 2007; Vicca et al., 2012), the variation of soil N availability with increasing age does not show a universal pattern (Ryan, Binkley, & Fownes, 1997; Yang, Luo, & Finzi, 2011). Compared with hydraulic limitation, soil N availability exhibits more complex age dynamics due to differences in litter quality, decomposition rates, and potential N losses between evergreen forests and deciduous forests (Mueller, Hobbie, Oleksyn, Reich, & Eissenstat, 2012; Takashima, Hikosaka, & Hirose, 2004). If hydraulic limitation is the dominant factor, the degradation of forest RUEs with age may be inevitable unless forest management reduced stand-level limits by removing taller trees. However, if the age-dependent changes in photosynthetic capacity and RUEs mostly depend on N availability, it is possible to improve forest productivity, decrease growth costs, and lengthen economic rotations by adjusting feedbacks among nutrient supplies, RUEs, and A_{max}.

In this study, we combined the FLUXNET and AmeriFlux flux observations, ancillary meteorological data, and site information from 62 forest sites in temperate regions to examine how temperate forest RUEs change with stand age and to understand the underlying regulatory mechanisms. Our specific objectives are to (a) identify the age patterns of temperate forest RUEs, (b) explore the relative importance of the regulatory variables to the variability of RUEs across temperate forests, and (c) reveal changes of soil N availability with forest aging after maturity in different forest types.

2 | MATERIALS AND METHODS

2.1 | Site selection and information

The sites were selected from the FLUXNET2015 Tier-1 and AmeriFlux sites located in temperate latitudes (23°26′N–66°34′N and 23°26′S–66°34′S) using the following criteria: (a) each site is a forest in which at least 80% of the trees are of the same lifeform (evergreen or deciduous) rather than a mixed forest, (b) stand age information was available, and (c) no severe disturbances (e.g., clearcutting, fire, and serious disease or insect outbreaks) occurred since the last stand-replacing disturbance. Of all 62 temperate forest sites with age ranging from 2 to 475 years old, 46 are evergreen forests consisting of seven evergreen broadleaved forests and 39 evergreen needle-leaved forests, and 16 are deciduous broadleaved forests. Although it was impossible with the data available to conduct an ideal comparative study by including the same age range, the range for evergreen and deciduous forests was still wide enough to warrant careful scientific scrutiny. The site information available included stand age, mean annual temperature, mean annual precipitation, aboveground biomass (AGB), and management (managed or unmanaged forests; Table S1). These site characteristics were collected from the biological, ancillary, disturbance, and metadata data and the published literature. Soil nutrient condition (SNC) for plant growth depends on multiple factors, such as soil texture, soil organic matter, soil organic carbon, soil total nitrogen (STN) in the top soils (i.e., 0–20 cm), pH, and carbon-to-nitrogen ratio (C:N; Vicca et al., 2012). In this study, we classified the site SNC into two levels: high- and low-nutrient availability (Table S2) based on the soil nutrient information following a classification scheme (Fernández-Martínez, Vicca, Janssens, Sardans, et al., 2014). Since there was no consistent age threshold for immature and mature forests in temperate regions (Martin et al., 2016), we divided temperate forests into immature and mature forests based on the dynamics of AGB with stand age (Kutsch et al., 2009). Generally, AGB does not significantly increase after maturity, and thus the forests over 90 years old were regarded as mature forests (Figure 1).

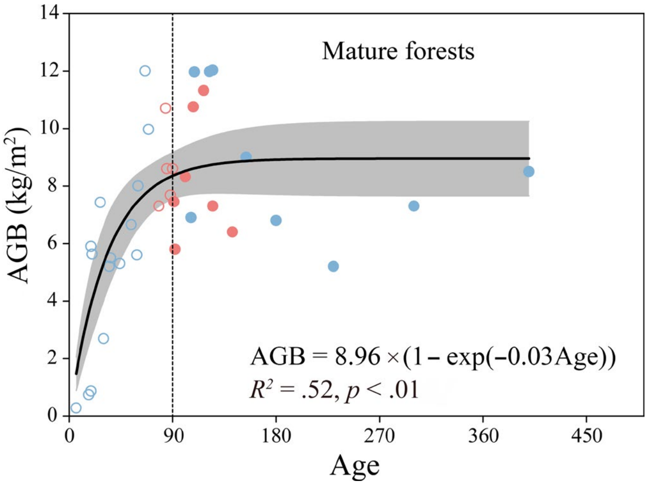

FIGURE 1 Dynamics of aboveground biomass (AGB) with stand age (Age) for the temperate forests. The blue circles and red circles represent evergreen forests and deciduous forests, respectively. Filled circles indicate the mature forests. The gray area around the regression line stands for the 95% confidence interval. Biomass data were not available for all flux sites, and only the sites with AGB data were plotted [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Flux data processing

The eddy covariance (EC) technique is the most common method of measuring net CO_2 and water vapor fluxes between terrestrial ecosystems and the atmosphere (Baldocchi, 2020). For the FLUXNET sites, the gap-filled and partitioned flux data and meteorological data were obtained from the FLUXNET2015 Dataset (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/). Flux data processing was performed following a standard and uniform data processing pipeline, including spike detection, data flagging, and friction velocity filtering (Papale et al., 2006). Half-hourly gross primary productivity (GPP) was calculated as the difference between measured net ecosystem exchange (NEE) and modeled ecosystem respiration (ER). We used the GPP estimated by a nighttime approach based on short-term temperature sensitivity (Reichstein et al., 2005). The AmeriFlux Dataset (https://ameriflux.lbl.gov/data/download-data/) provides raw flux data of the North, Central, and South American sites. For the AmeriFlux sites, we partitioned NEE into GPP and ER using a standard FLUXNET online flux-partitioning tool (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/), the same method used in the FLUXNET2015 Dataset.

2.3 | Estimation of RUEs

Ecosystem RUEs comprise indices of LUE and inherent water use efficiency (IWUE) in this study. The chronosequence of nitrogen use efficiency was not included because foliage or plant nitrogen content was not measured for many flux sites. At the canopy scale, LUE (g C/MJ PAR) was calculated as the ratio of GPP (g C/m^2) to the absorbed photosynthetically active radiation (APAR, MJ/m^2) that was the incident photosynthetically active radiation (PAR) absorbed by vegetation canopies as follows:

$$\mathrm{LUE} = \frac{\mathrm{GPP}}{\mathrm{APAR}} = \frac{\mathrm{GPP}}{\mathrm{FPAR} \cdot \mathrm{PAR}}, \tag{1}$$

where FPAR is the fraction of the PAR absorbed by the canopy, which was derived from the MODIS Collection 6 LAI/FPAR product (i.e., MOD15A2) at 500 m spatial resolution and 8 day temporal resolution (Myneni et al., 2002). The MODIS FPAR values described the observed values well at flux sites and thus represented FPAR for each ecosystem (Figure S1). The units of the measured PAR (μmol m^{-2} s^{-1}) were converted to J m^{-2} s^{-1} based on a conversion factor of 0.25 J/μmol (Chasmer et al., 2008; Liu et al., 2019).

Given the strong correlation between transpiration (or evapotranspiration) and atmospheric vapor pressure deficit (VPD), IWUE is considered to be more appropriate for studying the response of the efficiency of ecosystem water use to biophysical variables across meteorological conditions or biomes (Keenan et al., 2013; Tan et al., 2015). IWUE (g C kPa/kg H_2O) was expressed as follows (Beer et al., 2009):

$$\mathrm{IWUE} = \frac{\mathrm{GPP} \cdot \mathrm{VPD}}{\mathrm{ET}}. \tag{2}$$

The multiple-year average values of LUE and IWUE during the growing seasons (i.e., April–October in the northern hemisphere and October–April of the following year in the southern hemisphere) were calculated as the measures of RUEs at each site. To avoid uncertainty caused by insufficient turbulence at sunrise, half-hourly data at solar shortwave radiation (R_g) > 100 W/m^2 were used to estimate LUE and IWUE (Aubinet, Vesala, & Papale, 2012; Liu et al., 2019). LUE was calculated using the sums of half-hourly GPP and PAR and mean FPAR during each growing season. Similarly, the calculation of IWUE was based on the sums of half-hourly GPP and ET and mean VPD for each growing season.

2.4 | Biophysical parameters

The maximum photosynthetic capacity (P_{max}) was used to measure ecosystem photosynthetic productivity under light-saturated conditions (Fleischer et al., 2013; Smith et al., 2019). The response of photosynthetic productivity to PAR is commonly modeled by the Michaelis–Menten or Mitscherlich equation (Aubinet et al., 2012). We used the rectangle hyperbola equation, known as the Michaelis–Menten photosynthetic response model, to simulate the process of canopy-level photosynthesis and estimate P_{max} due to its widespread use in ecosystem-scale studies (Cabral et al., 2011; Xu, Zhang, Chen, Zhu, & Kang, 2017; Zhou et al., 2013) as follows:

$$\mathrm{GPP} = \frac{\alpha P_{max}\mathrm{PAR}}{\alpha \mathrm{PAR} + P_{max}}, \tag{3}$$

where α is the apparent quantum yield (μmol·CO$_2$/μmol PAR) and P_{max} is the ecosystem maximum photosynthetic capacity at the light-saturated conditions (μmol m^{-2} s^{-1}). Only daytime (i.e., PAR > 4 μmol m^{-2} s^{-1}) half-hourly data were used to fit the model, and the growing season P_{max} during the study period was considered constant at each site (Kljun et al., 2007). However, P_{max} may not reflect the actual A_{max} because the fitted curves may not saturate in many cases (Aubinet et al., 2012). We defined the GPP at a PAR of 2,000 μmol m^{-2} s^{-1} as A_{max} based on Equation (3) for all study sites (Koyama & Kikuzawa, 2010; Peri, Moot, & McNeil, 2005). Also, we found consistency between the A_{max} estimated by this method and the A_{max} fitted by the Mitscherlich light response model (Figure S2; Lindroth, Klemedtsson, Grelle, Weslien, & Langvall, 2008).

Canopy-integrated stomatal conductance can be represented by canopy conductance (G_c, mm/s), which was calculated by the inversion of the Penman–Monteith equation (Monteith & Unsworth, 1990) as follows:

$$G_c^{-1} = \frac{\rho_a C_p \left(\frac{\mathrm{VPD}}{\mathrm{LE}}\right)}{\gamma} + \left(\frac{\Delta}{\gamma}\beta - 1\right) g_a^{-1}, \tag{4}$$

$$g_a^{-1} = \frac{\mu}{\mu_*^2} + 6.2\mu_*^{-2/3}, \tag{5}$$

where ρ_a is the air density (kg/m), C_p is the specific heat capacity of air (J kg/K), VPD is the atmospheric vapor pressure deficit (kPa), LE is the latent heat (W/m^2), γ is the psychrometric constant (kPa/K), Δ is the slope of the saturation vapor pressure curve (kPa/K), β is the ratio of sensible heat to latent heat (i.e., Bowen ratio), g_a is the aerodynamic conductance (mm/s), μ is the wind speed (m/s), and μ^* is the friction velocity (m/s). All bulk surface parameters were calculated under the reference meteorological conditions (i.e., R_g ≥ 400 W/m^2, u ≥ 1 m/s, precipitation = 0 during past 10 hr; Granier, Biron, & Lemoine, 2000).

The variation of hydraulic limitation with stand age was estimated based on both AGB and the reference canopy conductance (G_{cref}). G_{cref} is the canopy conductance at VPD = 1 kPa under the reference meteorological conditions, which is highly related to canopy height and plant hydraulic conductance and thus could be used to test the "hydraulic limitation hypothesis" (Drake et al., 2010; Irvine et al., 2004; Novick et al., 2009). The half-hourly data were classified into VPD intervals of 0.2 kPa, starting at 0.6 kPa. For each VPD interval, the sum of average G_c and one standard deviation was calculated to represent the upper envelope of the data clouds (Herbst, Rosier, Morecroft, & Gowlng, 2008). The upper envelopes represented the possible G_c at optimal conditions, indicating that only VPD regulated G_c at the canopy scale. G_{cref} was obtained by fitting the upper envelopes according to a widely adopted empirical equation (Oren et al., 1999):

$$G_c = -m \cdot \ln(\mathrm{VPD}) + G_{cref}, \tag{6}$$

where G_{cref} is the G_c at VPD = 1 kPa, and m is the sensitivity of the canopy stomatal response to VPD.

2.5 | Statistical analysis

We averaged the site-level data over multiple years for each site and used the "space for time" method to explore the age patterns of RUEs for evergreen forests and deciduous forests, respectively. A gamma (Γ) function, an exponential function, and a Michaelis–Menten function were used to fit the age patterns of RUEs for temperate evergreen forests separately (Table S3; Besnard et al., 2018; Tang et al., 2014). The maximum likelihood method was applied to calculate the fitting parameters. The Akaike information criterion (AIC) was adopted to choose the best fitting model based on the root-mean-squared error (RMSE), sample size (n), and the number of the model parameter (P). When n is less than 40 times P (i.e., $n/P < 40$), the corrected AIC (AIC$_c$) was calculated as follows (Burnham & Anderson, 2002):

$$\mathrm{AIC}_c = n\log\sigma^2 + 2P + \frac{2P(P+1)}{n-P-1}. \tag{7}$$

The model that had the highest coefficient of determination (R^2) and minimum AIC$_c$ was adopted as the best model.

TheCook's distance was used to evaluate the influence of each data point on the fitted model (Cook, 1977) because the age distribution of temperate forests was not even, and there were few old-growth forests. The Cook's distance was estimated as follows:

$$D_{\mathrm{i}}=\frac{\sum_{j=1}^{n}\left(\widehat{Y}_j-\widehat{Y}_{j(i)}\right)^2}{P\cdot \mathrm{MSE}}, \tag{8}$$

where D_{i} is the Cook's distance of data point i, $\widehat{Y}_j$ is the predicted value for data point j from the model, $\widehat{Y}_{j(i)}$ is the predicted value for point j where point i has been excluded, P is the number of model parameters, and MSE is the mean square error or the square of RMSE. The Cook's distance has been extensively used for filtering high influence data points, and a value greater than three times the mean of the Cook's distance was regarded as the threshold to identify outliers (Adams et al., 2017; Tang et al., 2014).

We included the mean growing season temperature (MGT), mean growing season precipitation (MGP), ecosystem biological features (e.g., LAI and A_{max}), SNC, and forest age stage (FAS, maturity or immaturity) into multiple linear regression models to examine the effects of the various variables on the age pattern of RUEs for a certain forest type. We also tested the interactions up to the second order among A_{max}, SNC, LAI, and FAS to quantify and compare the relative contributions of these various predictors on forest RUEs during different age stages. The initial model was RUE ~ A_{max} + LAI + MGP + MGT + SNC + FAS + A_{max} × FAS + SNC × FAS + LAI × FAS. The "MuMIn" package in R (version 3.6.1) was used to simplify models by comparing $\mathrm{AIC}_{\mathrm{c}}$ values (Barton, 2012). If the difference between the two model $\mathrm{AIC}_{\mathrm{c}}$ values was less than 2, the models were not significantly different (Burnham & Anderson, 2002; Jones et al., 2019). After the selection of the final model, we used the averaging over orderings method (i.e., lmg) to evaluate the relative importance of each variable in the linear models by decomposing the R^2 value into non-negative contributions (Johnson, 2000). This calculation was implemented with the "relaimpo" package in R (Grömping, 2006). To test the difference in the relationship between A_{max} and STN or G_{c} between evergreen forests and deciduous forests, an analysis of covariance (ANCOVA) was performed. The Pearson correlation analysis was conducted to evaluate the coefficient of correlation (r) between two variables. All regression models were statistically assessed at a significance level of .05.

3 | RESULTS

3.1 | Age dynamics of temperate forest RUEs

Forest RUEs showed different age patterns between different forest types (Figure 2). Specifically, RUEs rapidly rose till reaching a peak at approximately 90 years and then gradually decreased with age for temperate evergreen forests. Evergreen forest LUE exhibited significant fluctuations with age, ranging from 0.55 ± 0.12 (±*SD*) at the age of 400 to 1.54 ± 0.05 g C/MJ PAR observed in a 65-year-old forest. For temperate evergreen forests, the mean IWUE during the growing season was 2.78 ± 0.10 g C kPa/kg H_2O. By contrast, deciduous forest RUEs continuously increased with age, at least to the maximum age available within the dataset. Age accounted for 69% and 54% of the variance in LUE and IWUE, respectively, in deciduous forests. The linear increase in LUE was statistically significant ($p < .01$), with an average of 1.11 ± 0.05 g C/MJ PAR across the deciduous sites. LUE and IWUE were strongly correlated across all sites ($R^2 = .38$, $p < .01$).

A gamma (Γ) function better described the age-related variation of RUEs across temperate forests than two prevailing models (Table S3). Although LUE and IWUE values from old evergreen forests (i.e., age > 200 years old) were included in the regressions, none were highly influential statistically (Table S4). Also, most data points representing old forests were within the 95% confidence intervals of the regressions. Following the models, stand age accounted for 42% and

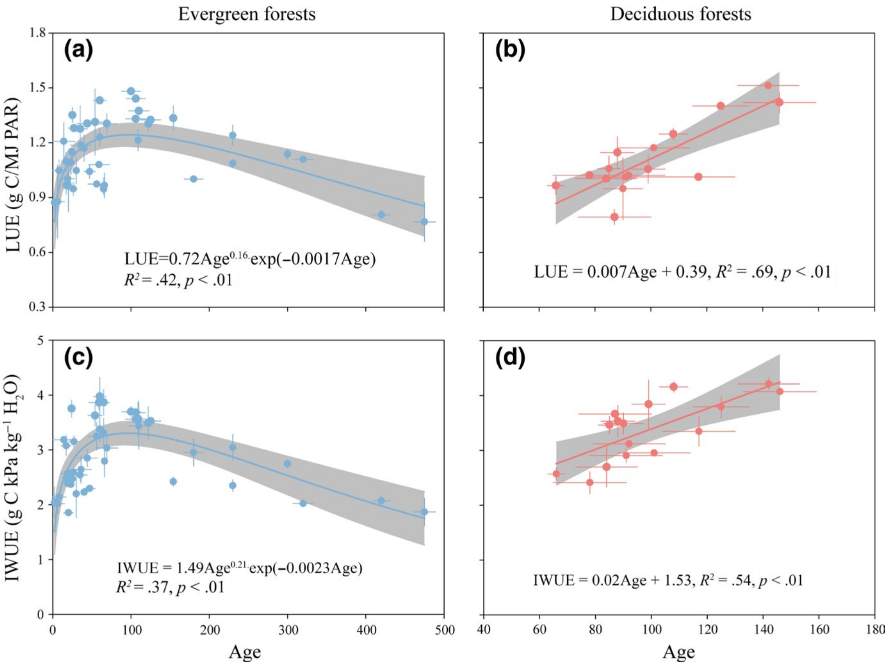

FIGURE 2 Ecosystem-level mean light use efficiency (LUE; a and b) and inherent water use efficiency (IWUE; c and d) over the growing seasons versus stand age (Age) for evergreen forests (blue circles) and deciduous forests (red circles) in temperate regions. The vertical bars indicate the standard errors of multi-year mean resource use efficiencies (RUEs) during the growing season. The horizontal bars represent the study years at each flux site. The blue and red solid lines indicate the fitted equations for evergreen forests and deciduous forests, respectively, and the gray shades are the 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

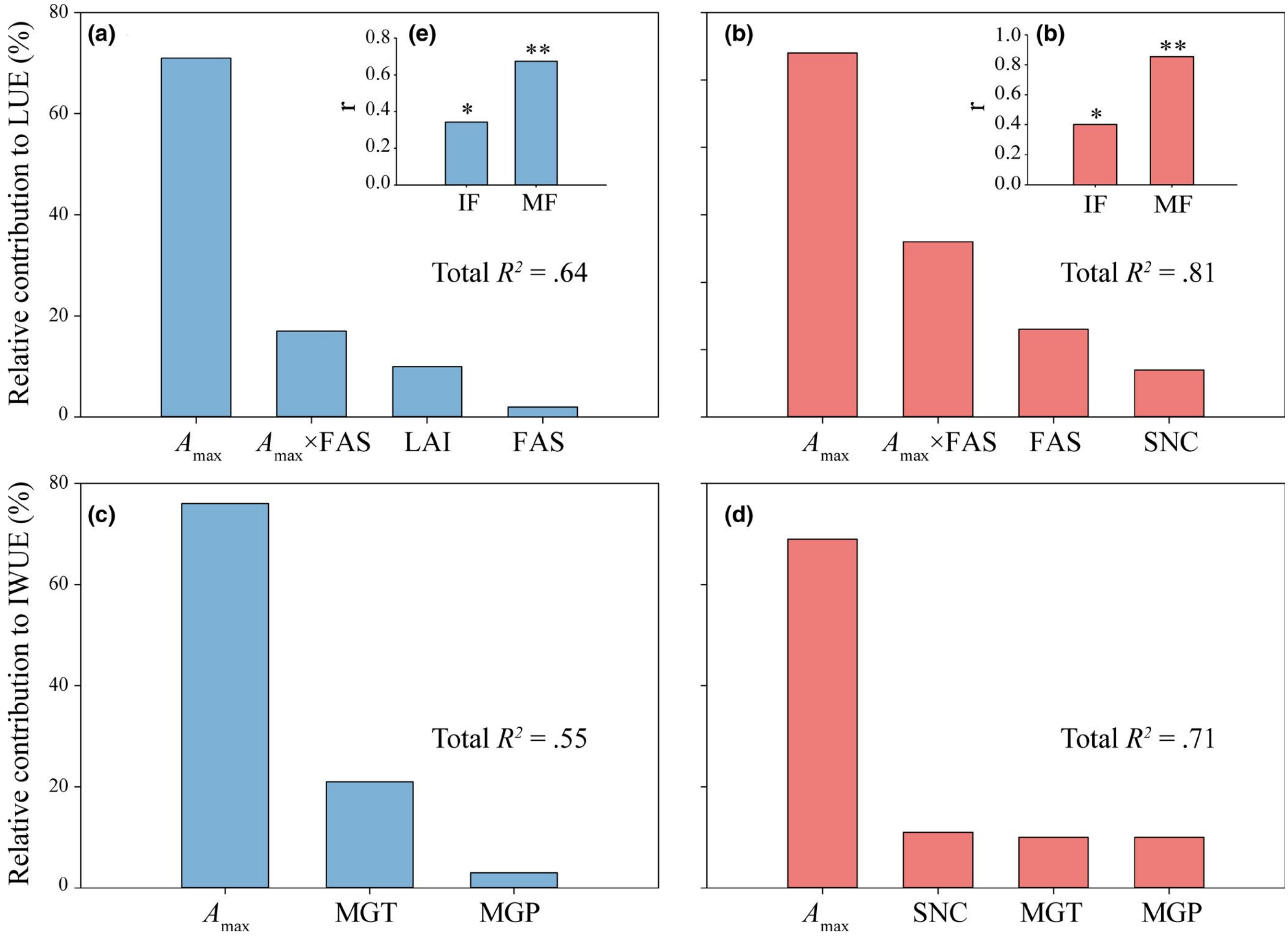

FIGURE 3 Relative contributions of selected variables to light use efficiency (LUE; a and b) and inherent water use efficiency (IWUE; c and d) for evergreen forests (blue bars) and deciduous forests (red bars). The "×" symbol indicates an interaction effect. Panel (e) and (f) represent the correlation coefficient (*r*) between LUE and A_{max} for immature forests (IF) and mature forests (MF). '*' and '**' indicate statistical significance at the level of 0.05 and 0.01, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

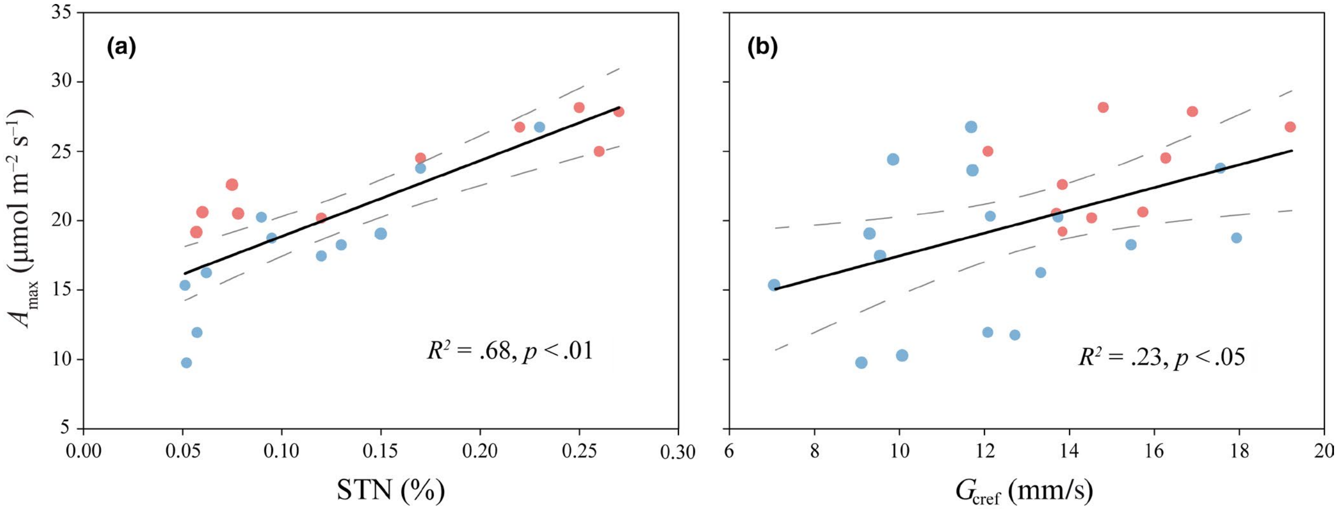

FIGURE 4 Relationship between canopy photosynthetic capacity (A_{max}) and soil total nitrogen (STN) at 0–20 cm (a) and reference canopy conductance (G_{cref}; b) for the mature evergreen forests (blue) and deciduous forests (red) in temperate zones. The black lines are fitted regression lines across two forest types, and the grey dashed lines indicate the 95% confidence intervals. Only the forest sites with STN data available were plotted in panel(a) [Colour figure can be viewed at wileyonlinelibrary.com]

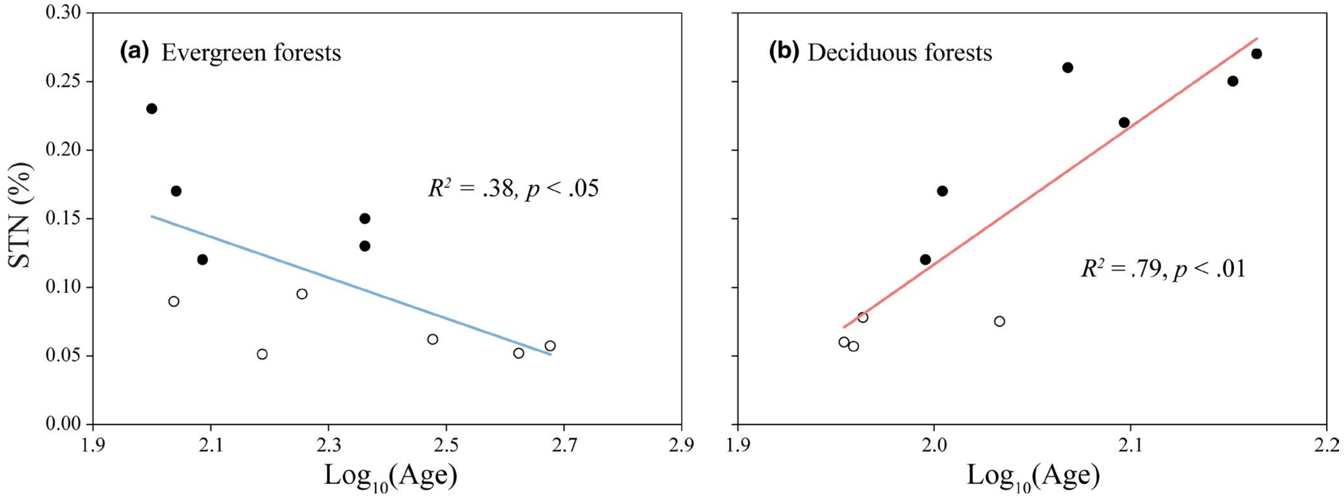

FIGURE 5 Relationship between soil total nitrogen (STN) at 0–20 cm and the logarithm of stand age (Age) for mature evergreen forests (a) and mature deciduous forests (b), respectively. The filled and hollow circles indicate high- and low soil nutrient conditions (SNCs), respectively. The blue and red lines stand for the fitted regressions across SNCs for mature evergreen and deciduous forests, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

37% of the variance in LUE and IWUE, respectively. For evergreen forests, the fitted regression model showed a maximum LUE of 1.27 (1.18–1.36, 95% confidence interval) g C/MJ PAR when 94 years old. Coincidentally, the peak value of modeled IWUE (3.12 g C kPa/kg H_2O) was observed at a similar age (91 years old) for evergreen forests.

3.2 | Regulatory mechanisms of RUEs across temperate forests

The relative contribution of a given variable to the variance in LUE and IWUE across temperate forest sites varied by forest type and age stage (Figure 3; Table S5). Overall, A_{max} was the dominant variable influencing RUEs across temperate sites regardless of the FAS (i.e., immature and mature stages). For evergreen forests, 46% and 44% of the variance in LUE and IWUE, respectively, could be explained by A_{max} alone. There was a significant interaction between A_{max} and FAS for LUE in both evergreen and deciduous forests ($p < .05$), and a stronger correlation was found at the mature stage (Figure 3e,f). When the additional interaction was included, A_{max} explained 56% of the variability in LUE. For temperate deciduous forests, A_{max} accounted for 65% of the variance in LUE when summed with its interaction with FAS (21%).

Moreover, SNC was significantly correlated with LUE and IWUE for the deciduous forests with a relative contribution of 0.07 and 0.11, respectively (Figure 3); however, it was excluded from the final models for the evergreens by the variable selection procedure. LAI was a significant variable only for evergreen forest LUE, and the relative contribution was low. Besides, there were no significant differences in RUEs between managed and unmanaged forests in temperate regions ($p > .05$; Figure S3). Temperate forest IWUE was more susceptible to climate variables (i.e., MGT and MGP) than LUE. It is worth mentioning that biological characteristics were more important for the variations of RUEs across temperate forests compared with climatic variables.

3.3 | Nitrogen regulation and hydraulic limitation on A_{max}

For the temperate forests older than 90 years, STN and G_{cref} played positive roles in regulating A_{max} (Figure 4), and there was no significant difference in the sensitivities between the two forest types (ANCOVA, $p > .05$). Across mature forests of both types, STN and G_{cref} accounted for 67% and 20% of the variance in A_{max}, respectively (Figure 4). STN declined linearly with stand age for mature evergreen forests but increased with age for mature deciduous forests regardless of SNC (Figure 5). The variation of STN with stand age was more evident at high-nutrient sites than at low-nutrient sites. By contrast, G_{cref} did not exhibit strong age-related variation after temperate forest matured (Figure S4). Coincidentally, AGB increased rapidly with stand age and then leveled off when stand age exceeded ~90 years (Figure 1).

4 | DISCUSSION

This study found that there are divergent age-related patterns in RUEs between temperate evergreen forests and deciduous forests in their mature stages. The age patterns of RUEs followed single-peak curves for temperate evergreen forests. Evergreen forest NEP reached a maximum at about 76 (69–83, 95% confidence interval) years, which was similar to the age of the growth peak in temperate forests reported elsewhere (Besnard et al., 2018; Tang et al., 2014). Although the temporal patterns of evergreen forest RUEs and growth followed the same age dynamics model, the peak age of forest growth occurred significantly earlier than that of maximum RUEs ($p < .05$), probably owing to the age dynamics of autotrophic respiration (Ryan et al., 1997; Tang et al., 2014). In contrast, the RUEs of deciduous forests exhibited continuously increasing trends with age, at least up to the maximum age available in the dataset. We cannot conclude whether deciduous forests continue to increase beyond the ages available here, or if they, too, will eventually decline, albeit just at a later age than evergreen forests. More old-growth forest sites with EC flux measurements and a more open data sharing policy are needed. Because older temperate conifer forests have lower RUEs, forest management may prioritize practices targeting their renewal. The finding that RUEs showed consistent age patterns for the same forest type also suggests strong coupling between LUE and IWUE (evergreen forests: $r = .71$, $p < .01$; deciduous forests: $r = .62$, $p < .01$) over the long-term scale (Fernández-Martínez, Vicca, Janssens, Luyssaert, et al., 2014; Goetz & Prince, 1999). Both stand age and forest type are important parameters for assessing ecosystem functions because forest RUE and carbon sequestration are considered as long-term measures of forest sustainability and resilience.

$A_{\max}$ was the primary factor determining the age-related change in RUEs. At an ecosystem scale, $A_{\max}$ represents the maximum photosynthetic capacity that trees can achieve under optimal environmental conditions (Fleischer et al., 2013; Kattge, Knorr, Raddatz, & Wirth, 2009). $A_{\max}$ varies by forest age and forest types and is restricted by hydraulic conductance, and soil/leaf nitrogen concentration (Bond, 2000; Kattge et al., 2009; Musavi et al., 2017). For mature temperate forests, the age-related pattern of $A_{\max}$ was related to soil N instead of the hydraulic limitation (Drake et al., 2010; Ryan et al., 2006). Hydraulic limitation is mostly a function of tree height, branch length, and biomass (Baret et al., 2018; Ryan et al., 2006). On one hand, the AGB accumulation gradually slowed down and then stabilized with stand age, and most temperate forests reach a maximum height during mid-succession (Ryan & Yoder, 1997). On the other hand, increased sapwood conductivity, enhanced tolerance for lower midday leaf water potential, and higher cavitation resistance along with tree age could offset the adverse effects of decreasing hydraulic conductance (Niinemets, 2002; Woodruff, Meinzer, & Lachenbruch, 2008).

Our results were consistent with the hypothesis that mature forest RUEs would be maintained, decreased, or increased based on the resource availability for trees (Fernández & Gyenge, 2009). Foliar N is tightly related to available soil N (Ollinger et al., 2002; Walker et al., 2014), and there is a strong positive correlation between N availability and the light-saturated rate of photosynthesis, particularly in temperate forests (LeBauer & Treseder, 2008; Ollinger et al., 2008). Furthermore, Ollinger et al. (2002) found that, in deciduous forests of New Hampshire, both foliar N and soil N availability were higher in old-growth forests than previously disturbed forests, but that the reverse was true in needle-leaf evergreen forests. They attributed this pattern to long-term plant–soil feedbacks that increase or decrease soil N availability over time as a function of leaf litter chemistry. Our results are consistent with this hypothesis. They do not, however, support the idea of N oligotrophication processes in forests (Craine et al., 2018; Groffman et al., 2018). This does not indicate that N oligotrophication does not occur, but suggests that it is either not a dominant process for sites included in this study, or that the space-for-time chronosequence approach used here is not sufficient for identifying it.

LUE and IWUE, two RUEs influenced by soil N, declined in mature evergreen forests after reaching a peak but continued to increase in deciduous forests. There are several possible explanations for this result. First, because more N is immobilized in woody litter and dead trees as floor litters accumulate, N stored in litters may not represent available nutrition during a relatively short period in temperate regions (Johnson, 2006; Murty & McMurtrie, 2000). Second, leaf mass per area (LMA) increases with age (Steppe et al., 2011), which corresponds to less N investment in photosynthetic apparatus (Poorter, Remkes, & Lambers, 1990). Third, plants have profound impacts on soil N availability over time, and the effects depend on litter chemistry and net N mineralization rate ($N_{\min}$; Berendse & Scheffer, 2009; Mueller et al., 2012). Generally, evergreen species invest more N in cell walls and leaf structural tissues to increase leaf longevity and LMA, while deciduous species prioritize photosynthetic tissues (Takashima et al., 2004). Deciduous forests usually have high-quality litters, which result in higher $N_{\min}$ than evergreen forests (Cornwell et al., 2008). Therefore, deciduous trees can increase soil fertility over time, and delay forest functional decline (Forrester, Collopy, Beadle, & Baker, 2013; Vitousek, 1982).

Furthermore, our work supports the idea that RUEs are more dependent on SNC for deciduous forests than for evergreen forests. This is because a considerate portion of internal nutrients is lost during the defoliation for deciduous trees, and thus more soil nutrients are needed for the leaf growth next year. By contrast, leaf senescence is often accompanied by new growth for evergreen species, allowing direct nutrient recycling from old to new leaves, which results in less sensitivity to soil nutrients (Aerts & Chapin, 1999; Nambiar & Fife, 1991).

5 | CONCLUSIONS

We explored the chronosequences of temperate forest RUEs and the regulatory mechanisms based on data obtained from the FLUXNET2015 and AmeriFlux datasets and published literature. We found different RUE patterns in evergreen and deciduous forests. In evergreen forests, RUEs for light and water increased to a stand age of ~90 years and then gradually declined. However, in deciduous forests, these RUEs continued to increase with stand age. $A_{\max}$ was the dominant factor controlling the age patterns of RUEs across temperate forest sites. The age-related change in soil N availability is likely the mechanism regulating the age dynamics of $A_{\max}$ in mature and postmature temperate forests. Specifically, STN for evergreen forests decreased over time, while for deciduous forests it increased with age due to higher litter quality and $N_{\min}$. RUEs were more sensitive to SNCs for deciduous forests than for evergreen forests because the latter has tighter internal nutrient cyclings. For mature temperate forests, G_{cref} and AGB did not show significant changes with age, indicating that hydraulic limitations may not be a factor affecting the age patterns of mature forest RUEs in temperate zones. Overall, stand age and forest type played prominent roles in regulating temperate forest RUEs. Accordingly, age-related biological changes must be considered when evaluating forest functional response to a changing climate and managing forest productivity.

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AUTHOR CONTRIBUTION

J.X., H.X., and Z.Z. designed the research. H.X., J.X., and J.W. collected data and conducted the analysis. H.X., J.X., Z.Z., S.V.O., D.Y.H., and Y.P. interpreted the results and wrote the paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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