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Steeper declines in forest photosynthesis than respiration explain age-driven decreases in forest growth

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The traditional view of forest dynamics originated by Kira and Shidei [Kira T, Shidei T (1967) Jap J Ecol 17:70–87] and Odum [Odum EP (1969) Science 164(3877):262–270] suggests a decline in net primary productivity (NPP) in aging forests due to stabilized gross primary productivity (GPP) and continuously increased autotrophic respiration (R a). The validity of these trends in GPP and R a is, however, very difficult to test because of the lack of long-term ecosystem-scale field observations of both GPP and R a. Ryan and colleagues [Ryan MG, Binkley D, Fownes JH (1997) Ad Ecol Res 27:213–262] have proposed an alternative hypothesis drawn from site-specific results that aboveground respiration and belowground allocation decreased in aging forests. Here, we analyzed data from a recently assembled global database of carbon fluxes and show that the classical view of the mechanisms underlying the age-driven decline in forest NPP is incorrect and thus support Ryan’s alternative hypothesis. Our results substantiate the age-driven decline in NPP, but in contrast to the traditional view, both GPP and R a decline in aging boreal and temperate forests. We find that the decline in NPP in aging forests is primarily driven by GPP, which decreases more rapidly with increasing age than R a does, but the ratio of NPP/GPP remains approximately constant within a biome. Our analytical models describing forest succession suggest that dynamic forest ecosystem models that follow the traditional paradigm need to be revisited.

Significance

Advancing our understanding of how and why forests dynamically change in their productivity is important to predict the future change. The traditional view of forest dynamics originated by Kira, Shidei, and Odum suggests a decline in net primary productivity [or gross primary productivity (GPP)] – autotrophic respiration (R a) in aging forests due to stabilized GPP and continuously increased R a. We found that, in contrast to the traditional view, both GPP and R a decline in aging forests while GPP decreases more rapidly than R a does, and thus generalize the alternative hypothesis initiated by Ryan and colleagues with a large dataset. We presented a new quantitative model to describe forest dynamics that can be incorporated into ecosystem models.

Author contributions: J.T. designed research; J.T., S.L., A.D.R., W.K., and I.A.J. performed research; J.T. contributed new reagents/analytic tools; J.T. and S.L. analyzed data; and J.T. wrote the paper.

The authors declare no conflict of interest.

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most second-growth forests are in dynamic succession, lacking the ability to incorporate forest age into ecosystem and carbon cycle models as an important driver makes prediction of future ecosystems unrealistic. As a result, few ecosystem models have been able to include forest age or succession as an important variable (7). How to quantify the age effect on carbon dynamics is challenging in model development. Recent advancement of technology in carbon flux measurement has dramatically expanded our ability to quantify the ecosystem carbon budget from individual plants (e.g., ref. 13) to the landscape scale (14). As a result, more and more GPP, NPP, and \( R_a \) datasets are becoming available.

To revisit the classical ecological paradigm and generalize the alternative paradigm on the age-driven decline of forest productivity, we use a recently assembled extensive global dataset (15) to test (i) whether forest NPP declines in aging forests as a general trend across biomes, and (ii) whether the age-related decline in forest NPP is due to increasing respiration, as assumed in the paradigm, or is instead primarily due to decreasing GPP. We intend to propose an analytical model to explain the age-driven change in forest productivity and respiration.

**Results and Discussion**

The age patterns of NPP for temperate and boreal forests agree with the classical model, i.e., following a stand-replacing disturbance, NPP initially increases, reaches a maximum at maturity, and then decreases with further forest aging (Fig. 2). The fitted \( \Gamma \) functions are highly statistically significant (\( t \) tests and \( F \) tests), but exhibit low \( R^2 \) (Table 1). These low \( R^2 \) values were expected given the strong dependence of NPP on other factors such as climate, soil fertility, disturbances, management history, etc. (15, 16). Among the five models that were compared (the second-degree polynomial function, the third-degree polynomial function, the logarithmic function, the Michaelis–Menten function, and the \( \Gamma \) function), the \( \Gamma \) function had the best overall performance (the lowest Akaike information criterion, or \( AIC_c \)) across the four datasets (temperate NPP vs. age, boreal NPP vs. age, temperate GPP vs. age, and boreal GPP vs. age). The rare NPP or GPP values from old forests (age > 300 y) were found to be important points in the regression lines, but none of them was statistically highly influential (\( D_i > 1; D_i \) is the Cook’s distance), and all were within the 95% confidence interval areas of the regressions. However, we are aware that the parameters of the functions may change if we have more data, particularly in older forests.

In boreal forests, the fitted regression model showed a maximum NPP at 340 (290–400, 95% confidence interval) g C m\(^{-2}\) y\(^{-1}\) around 100 y old. In temperate forests, the fitted maximum NPP amounted to 740 (680–800, 95% confidence interval) g C m\(^{-2}\) y\(^{-1}\) at ~70 y old. The higher maximum NPP and earlier maturity in temperate compared with boreal forests may be the consequence of the higher metabolic rates due to the higher mean annual temperature and also higher soil fertility in temperate forests.

Although the NPP data in our dataset agree with the observations upon which Kira and Shidei (9) developed their original hypothesis, the field observations of GPP and the derived \( R_a \) (calculated as GPP – NPP) do not follow the pattern assumed in the classical model (Fig. 3). In contrast to the earlier theorem, GPP does not stabilize at levels slightly below the maximum value at maturity, but declines far more than previously assumed. Potential mechanisms to explain the age-related decrease in GPP primarily include (i) nutrient limitation: soil nutrients, especially nitrogen, become increasingly immobilized in the organic surface horizon and in the N-rich, humified soil organic matter due to the accumulation of woody biomass (1); (ii) hydraulic limitation: hydraulic resistance increases with tree height, resulting in decreased stomatal conductance (3, 17, 18); and (iii) genetic control: reduced photosynthetic rates could be controlled by gene expression programmed in the meristematic cells in plant stems, resulting in diminishing metabolism rates in aging plants (19, 20). Although these mechanisms have been discussed and tested in a limited number of studies (1, 3), no consensus has yet been reached (21, 22).

Our results suggest that the NPP/GPP ratio varies considerably among forest biomes (Fig. 4). The difference in the NPP/GPP ratio between mature boreal and temperate forests is significant, as NPP/GPP ranging from 0.30 to 0.34 in boreal forests and 0.40 to 0.45 in temperate forests, analytically derived from the ratio of NPP/GPP with the parameters from Table 1 and Eq. 1. Paired GPP–NPP measurement data verified these results. NPP/GPP is significantly different between temperate and boreal forests (ANOVA, \( P < 0.01 \)) with mean values of 0.39 (\( \pm 0.13 \) SD, \( n = 17 \)).
in boreal forests and 0.49 (±0.11 SD, n = 28) in temperate forests. Vicca et al. (16) postulated that this large difference in NPP/GPP between boreal and temperate forests is mainly due to the typically higher fertility in temperate forests, where trees invest less photosynthates in nutrient acquisition mechanisms such as exudation or symbionts, leaving a higher fraction of GPP available for wood production.

Within both the boreal and temperate biomes, we observed a stable NPP/GPP ratio across age (Fig. 4). Paired GPP–NPP data indicate that the correlation between GPP/NPP and age is not significant (slope \( P > 0.05 \)) in both temperate and boreal forests. This constancy with age (two black lines in Fig. 4) contradicts with the original theorem, where the NPP/GPP ratio is expected to decrease with age because NPP declines and GPP stabilizes (the gray line in Fig. 4). Our observed trend of insensitivity of NPP/GPP to age within a biome but significant difference between boreal and temperate forests disagrees with previous publications that NPP/GPP decreases with age (23, 24). We also disagree with that NPP/GPP tends to be conservative across age classes and ecosystems (25–28) and agrees with the variability of NPP/GPP across ecosystems (23). Recent studies has shown that the NPP/GPP ratio could be influenced more by temperature (29) or by nutrient availability (16) than by age.

In the classical model, \( R_a \) would be expected to continue to increase as forests age (Fig. 1). Both our calculated \( R_a \) lines and measurement data contradict this classical hypothesis, with a decrease in \( R_a \) after maturity (Fig. 3), in agreement with findings of Ryan et al. (2, 3, 11). The primary explanation for the hypothesized continuous increase in respiration was that, although leaf respiration stabilizes with maximum leaf area index after canopy closure, wood respiration continues to increase with the accumulation of woody biomass in aging forests (9). In recent years, many studies have indicated the tight coupling between ecosystem GPP and respiration (30–33), which is not surprising given that plants cannot respire more than the available supply of recent or stored photosynthetic. This tight coupling between GPP and respiration not only substantiates the indication for a constant NPP/GPP ratio with age within a biome but also suggests that the decrease in GPP is the prime reason for the decline in \( R_a \). If the respiratory carbon cost is indeed a fixed proportion of GPP, then a reduction in GPP with age would be the main cause of the widely observed age-driven decline in NPP.

There are other mechanisms that uncouple respiration from accumulated biomass stocks in aging forests and could explain the reduction in \( R_a \) more mechanistically. If autotrophic respiration is partitioned into growth and maintenance respiration, the latter may increase with age due to the increase in standing biomass, but growth respiration would decline with the age-related decrease in NPP, perhaps offsetting the increase in maintenance respiration, and thus potentially resulting in a decrease in total autotrophic respiration (2). Moreover, leaf and root biomass are unlikely to increase with aging, and the respiratory sapwood only accounts for a small fraction of the accumulated woody biomass in aging forests. Hence, any age-related increase in maintenance respiration with increasing forest age is expected to be very limited. An empirical study has indeed shown that stem respiration in an old-growth hardwood stand decreased compared with young and mature stands in the Great Lakes area (13).

Because our results for age-related trends in GPP and \( R_a \) for both boreal and temperate forests oppose the traditional view of the mechanism underlying the age-related decline in forest NPP, we propose here a previously unidentified conceptual model (Fig. 5). This conceptual model, presented in terms of parameterized \( \Gamma \) functions, builds on that proposed earlier by Ryan et al. (2) but differs from both the classical model and this newer view in that we specify that the decrease in NPP results from the combined effects of (i) a decline in GPP with increasing age and (ii) an approximately constant NPP/GPP ratio independent of age, i.e., \( R_a \) follows the change in GPP but decreases more slowly with increasing age than GPP in aging forests. Our results suggest that the age effect on forest GPP, \( R_a \), and NPP, independent of climatic and edaphic controls and management practices, is of fundamental importance for understanding patterns of forest growth and carbon dynamics. Long-term forest ecosystem models must therefore also consider age as a dominant control on spatial and temporal patterns of forest productivity to realistically simulate carbon cycles. The ratio of NPP/GPP (and thus of \( R_a / \text{GPP} \)) is highly variable across biomes but appears independent of age in mature forests within a biome. The decline in NPP in aging forests is mainly driven by the reduction in GPP. The mechanism of reduced GPP with age needs further studies.

**Materials and Methods**

We used an established global database (15) of forest GPP and NPP, obtained from eddy covariance measurement (34, 35), chamber-based flux measurement,
biometric inventories, modeling results, and corresponding site properties and climatic parameters to investigate the age effect on GPP, NPP, R\textsubscript{a}, and NPP/GPP. The database was assembled from published literature, existing computer databases (36, 37), and the AmeriFlux and CarboEurope networks within the FLUXNET (38). NPP was typically measured by the sum of incremental biomass of forest woods and annual production of leaves and roots. Estimating NPP for roots is challenging (39) and allometric equations were derived from the modeled GPP and NPP using Eq. 1 and parameters from Table 1. The gray line is conceptual following Odum’s traditional model in Fig. 1.

We compiled a subset of the database by using only annual sums of GPP, NPP, R\textsubscript{a}, and age (years since regeneration after a major disturbance, e.g., harvest, fire, or land-use shift). We excluded any forest sites subject to major experimental or management treatments (e.g., elevated ambient CO\textsubscript{2} concentration, fertilization, thinning, and/or irrigation). We also averaged multiple years, where available, of GPP, NPP, and R\textsubscript{a} to obtain mean annual values. For those sites with different GPP values originating from multiple methods, we used only eddy covariance-derived GPP. Although reporting uncertainty is important (42), most individual datasets do not contain uncertainty levels. Based on the literature reports on eddy flux uncertainty (14, 43) and expert judgment (15), the uncertainty, varying among individual sites, was less than 30% for GPP and 20% for NPP for our dataset. We have not found any evidence that the uncertainty is correlated with forest age. We also acknowledge the uncertainty associated with the chronosequence approach (e.g., ref. 5) that we used to study the age effect on GPP, NPP, and R\textsubscript{a} given the variability of site conditions. Therefore, we grouped datasets by major biomes and assumed that this uncertainty associated with the chronosequence method is randomly distributed within a biome.

We categorized all forest sites into boreal, temperate, Mediterranean, and tropical biomes based on climatic characteristics and species mixtures. Due to limited measurement data in Mediterranean sites and tropical forests, in this study we only analyzed boreal and temperate sites. As a result, we obtained 73 sites with GPP data, 166 sites with NPP data, 17 sites with independently measured R\textsubscript{a} data (not calculated from GPP – NPP), and 45 paired GPP–NPP datasets all accompanied with age data (see Table S1 for details). Paired GPP–NPP data mean that both GPP and NPP were independently measured at one site at the same or close to the same year so that we could directly calculate the NPP/GPP ratio for this site.

We used a gamma (Γ) function (Eq. 1) to fit the age effect of GPP and NPP for both boreal and temperate biomes. This type of function has been used to describe the age-driven change of forest floor organic matter (44) even though the simplicity of the pattern has been challenged by field-based data (45):

$$y = k_0 t^a e^{b t},$$  

where y is GPP or NPP (in grams of carbon per square meter per year), t is the forest age (in years since the last major disturbance such as harvest or fire), and $k_0$, $k_1$, and $k_2$ are parameters. Eq. 1 could be log-transformed to a linear equation. Parameters in Eq. 1 were then estimated by conducting multivariate linear regression. Two sets of the Γ function for GPP and NPP, respectively, allowed us to analytically derive $R_a$ (GPP – NPP) and the ratio of NPP/GPP as a function of age. Independently measured NPP/GPP and $R_a$ data were used to validate the modeled results of NPP/GPP and $R_a$.

We determined the age at which maximum values of GPP and NPP were obtained by differentiating Eq. 1 (Eq. 2):

$$y_{max} = k_0 (−k_1/k_2)^{1/a}e^{−b/k_2}, \text{ when } t = −k_1/k_2.$$  

We also tested different functions to fit the data, including a second-degree polynomial function, a third-degree polynomial function, a logarithmic function, and a Michaelis–Menten function ($y = ax/(b + x)$). We used the root-mean-squared error (RMSE) to evaluate the model accuracy and efficiency. We also used the Akaike information criterion (AIC) to compare models as AIC considers both the lowest RMSE and the fewest model parameters, accounting for both goodness-of-fit and the complexity of the model (46, 47). When the number of parameters ($p$) is large comparing with the sample size ($n$) (generally $np < 40$), we used AIC, (Eq. 3) (47). The model with the lowest AIC is the best candidate:

$$AIC = n \log \sigma^2 + 2p + \frac{2p(p + 1)}{n − p − 1}.$$  

where $n$ is the number of observations, $\sigma$ is the RMSE, and $p$ is the number of parameters.

![Fig. 4. Changes in NPP/GPP with age in boreal and temperate forests. The dots are measurements from paired GPP–NPP data. The black lines are derived from the modeled GPP and NPP using Eq. 1 and parameters from Table 1. The gray line is conceptual following Odum’s traditional model in Fig. 1.](image)

![Fig. 5. Our model showing the decrease in NPP resulting from both decreases in GPP and $R_a$ in boreal (A) and temperate (B) forests, in contrast to Fig. 1. The GPP line and the gray area of NPP are fitted from measurement data (Eq. 1 and Table 1), and the $R_a$ line is derived from fitted GPP and NPP as GPP – NPP.](image)
Because the age data are not evenly distributed with less data in older forests, we used the “Cook distance” to estimate the influence of a data point (48), for example, in old-growth forests:

\[ D = \frac{\sum_{i=1}^{n} (\hat{y}_i - \bar{y}_i)\sqrt{n}}{\text{MSE}}, \]

where \( D \) is the Cook’s distance for data point \( i \), \( \hat{y}_i \) is the predicted value from the model for data point \( i \), \( \bar{y}_i \) is the predicted value for point \( j \) from the model in which point \( i \) has been omitted, \( n \) is the number of fitted parameters in the model, and \( \text{MSE} \) is the mean square error (deviation), or \( \text{RMSE}^2 \). The Cook’s distance considers both the \( x \) value and \( y \) value to evaluate if a data point is highly influential (an outlier). Although controversial, The point with \( D > 1 \) is considered a highly influential point (49). If there are points with substantially high \( D \) than others, we carefully recheck the points by comparing regression with and without these points and remove the points if they are outliers.