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

3   forest growth

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20 **Abstract**

21 The traditional view of forest dynamics originated by Kira, Shidei, and Odum suggests a

22 decline in net primary productivity (NPP) in ageing forests due to stabilized gross

23 primary productivity (GPP) and continuously increased autotrophic respiration (R_a). The

24 validity of these trends in GPP and R_a is, however, very difficult to test because of the

25 lack of long-term ecosystem-scale field observations of both GPP and R_a. Ryan and

26 colleagues have proposed an alternative hypothesis drawn from site-specific results that

27 aboveground respiration and belowground allocation decreased in ageing forests. Here

28 we analyzed data from a recently assembled global database of carbon fluxes and show

29 that the classical view of the mechanisms underlying the age-driven decline in forest NPP

30 is incorrect and thus support Ryan's alternative hypothesis. Our results substantiate the

31 age-driven decline in NPP, but in contrast to the traditional view, both GPP and R_a

32 decline in ageing boreal and temperate forests. We find that the decline in NPP in ageing

33 forests is primarily driven by GPP, which decreases more rapidly with increasing age

34 than R_a does, but the ratio of NPP/GPP remains approximately constant within a biome.

35 Our analytical models describing forest succession suggest that dynamic forest ecosystem

36 models that follow the traditional paradigm need to be revisited.

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38 **Key words:** Succession, chronosequence, forest dynamics, photosynthesis, respiration,

39 carbon flux, carbon use efficiency

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Significance Statement

Advancing our understanding 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 (NPP, or GPP - R_a) in ageing forests due to stabilized gross primary productivity (GPP) and continuously increased autotrophic respiration (R_a). We found that in contrast to the traditional view, both GPP and R_a decline in ageing 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.

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56   **Introduction**

57   It has been long observed and well established that forest net primary production

58   (NPP), particularly aboveground NPP, increases during initial stand development, peaks

59   at maturity, and then gradually declines as forests age (1-8). Kira and Shidei (9) were the

60   first to analyze 10 years of empirical data and developed the long-accepted theory that

61   forest NPP declines with age because wood respiration increases in response to the

62   accumulating wood biomass, while gross primary production (GPP) remains quasi-

63   constant (Fig. 1). Similarly, in his theory of ecosystem succession, Odum (10) postulated

64   that ecosystem respiration (i.e. the sum of autotrophic and heterotrophic respiration)

65   increases with age and eventually balances GPP such that the net ecosystem carbon

66   balance approaches zero at a dynamic steady state. Odum did not specify the successional

67   pattern of autotrophic respiration (R_a) and NPP, but the underlying assumption is similar

68   to that of Kira and Shidei, i.e., the difference between carbon uptake and release declines

69   with age primarily because respiratory losses increase.

70   Ryan et al. have disproved these earlier hypothesized patterns and contended that

71   total stem respiration, including growth and maintenance respiration, in a chronosequence

72   of subalpine lodgepole pine (*Pinus contorta* ssp. *latifolia*) stands in Colorado, USA did

73   not increase with forest age (11), and that the observed decrease in aboveground NPP

74   with increasing age in an experimental forest of *Eucalyptus saligna* in Hawaii, USA

75   originated from a decrease in GPP that overshadows a simultaneous decrease in the sum

76   of all carbon that is not used for aboveground NPP (i.e. aboveground respiration plus

77   belowground allocation) (3). Ryan et al. concluded that with forest aging, canopy

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78   photosynthesis decreases in company with a decline in aboveground production,

79   aboveground respiration, and belowground allocation (2). More recently, Drake et al. (6)

80   supported Ryan et al. (2, 3) by concluding that the decrease in NPP with age was driven

81   by the decrease in GPP and the companion decrease in R_a, a conclusion drawn from their

82   work conducted across a chronosequence of forest stands at the Duke Forest in North

83   Carolina, USA. However, with the widely used eddy covariance method and its

84   companion measurements of NPP and heterotrophic respiration, the classical hypothesis

85   was supported recently that the increasing R_a, rather than GPP, drove the decrease in NPP

86   along a chronosequence of boreal forest stands (12). Therefore, to empirically test

87   Odum's established theory and the generality of the alternative hypothesis proposed by

88   Ryan et al. (2, 3, 10) and supported by Drake et al. (6) through site-specific studies, more

89   measurement data across different biomes and ecosystems are needed to support if it is

90   because (A) GPP decreases but R_a increases with forest age, or (B) both GPP and R_a

91   decrease with age that results in the observed decrease in NPP with age.

92   Advancing our mechanistic understanding of the control of forest age on

93   ecosystem production and respiration has become more crucial during the past decades

94   because improving our ability to predict long-term ecosystem responses to global change

95   is urgently needed for making sound climate change policy. While most second-growth

96   forests are in dynamic succession, lacking the ability to incorporate forest age into

97   ecosystem and carbon cycle models as an important driver makes prediction of future

98   ecosystems unrealistic. As a result, few ecosystem models have been able to include

99   forest age or succession as an important variable (7). How to quantify the age effect on

100   carbon dynamics is challenging in model development. Recent advancement of

101   technology in carbon flux measurement has dramatically expanded our ability to quantify

102   the ecosystem carbon budget from individual plants (e.g. 13) to the landscape scale (14).

103   As a result, more and more GPP, NPP, and R_a datasets are becoming available.

104   To revisit the classical ecological paradigm and generalize the alternative

105   paradigm on the age-driven decline of forest productivity, we use a recently assembled

106   extensive global dataset (15) to test (A) whether forest NPP declines in ageing forests as

107   a general trend across biomes, and (B) whether the age-related decline in forest NPP is

108   due to increasing respiration, as assumed in the paradigm, or is instead primarily due to

109   decreasing GPP. We intend to propose a new analytical model to explain the age-driven

110   change in forest productivity and respiration.

111   **Results and discussion**

112   The age patterns of NPP for temperate and boreal forests agree with the classical

113   model, i.e., following a stand-replacing disturbance, NPP initially increases, reaches a

114   maximum at maturity, and then decreases with further forest ageing (Fig. 2). The fitted Γ

115   functions are highly statistically significant (t-tests and F-tests), but exhibit low R^2 (Table

116   1). These low R^2 values were expected given the strong dependence of NPP on other

117   factors such as climate, soil fertility, disturbances, management history, etc. (15, 16).

118   Among the five models that were compared (the second-degree polynomial function, the

119   third-degree polynomial function, the logarithmic function, the Michaelis-Menten

120   function, and the Γ function), the Γ function had the best overall performance (the lowest

121   Akaike Information Criterion, or AIC_c) across the four data sets (temperate NPP vs. age,

122   boreal NPP vs. age, temperate GPP vs. age, and boreal GPP vs. age). The rare NPP or

123   GPP values from old forests (age > 300 years) were found to be important points in the

124   regression lines, but none of them were statistically highly influential ($D_i > 1$, D_i is the

125   Cook's Distance) and all were within the 95% confidence interval areas of the

126   regressions. However, we are aware that the parameters of the functions may change if

127   we have more data, particularly in older forests.

128   In boreal forests, the fitted regression model showed a maximum NPP at 340 (290

129   – 400, 95% confidence interval) g C m^{-2} y^{-1} around 100 years old. In temperate forests,

130   the fitted maximum NPP amounted to 740 (680 – 800, 95% confidence interval) g C m^{-2}

131   y^{-1} at approximately 70 years old. The higher maximum NPP and earlier maturity in

132   temperate compared to boreal forests may be the consequence of the higher metabolic

133   rates due to the higher mean annual temperature and also higher soil fertility in temperate

134   forests.

135   Although the NPP data in our dataset agree with the observations upon which

136   Kira and Shidei (9) developed their original hypothesis, the field observations of GPP and

137   the derived R_a (calculated as GPP – NPP) do not follow the pattern assumed in the

138   classical model (Fig. 3). In contrast to the earlier theorem, GPP does not stabilize at

139   levels slightly below the maximum value at maturity, but declines far more than

140   previously assumed. Potential mechanisms to explain the age-related decrease in GPP

141   primarily include (A) nutrient limitation: soil nutrients, especially nitrogen, become

142   increasingly immobilized in the organic surface horizon and in the N-rich, humified soil

143   organic matter due to the accumulation of woody biomass (1); (B) hydraulic limitation:

144   hydraulic resistance increases with tree height, resulting in decreased stomatal

145   conductance (3, 17, 18); and (C) genetic control: reduced photosynthetic rates could be

146   controlled by gene expression programmed in the meristematic cells in plant stems,

147   resulting in diminishing metabolism rates in ageing plants (19, 20). While these

148   mechanisms have been discussed and tested in a limited number of studies (1, 3), no

149   consensus has yet been reached (21, 22).

150   Our results suggest that the NPP/GPP ratio varies considerably among forest

151   biomes (Fig. 4). The difference in the NPP/GPP ratio between mature boreal and

152   temperate forests is significant, as NPP/GPP ranging from 0.30 to 0.34 in boreal forests

153   and 0.40 to 0.45 in temperate forests, analytically derived from the ratio of NPP/GPP

154   with the parameters from Table 1 and Eq. 1. Paired GPP-NPP measurement data verified

155   these results. NPP/GPP is significantly different between temperate and boreal forests

156   (ANOVA, $p < 0.01$) with mean values of 0.39 ($\pm$ 0.13 SD, n = 17) in boreal forests and

157   0.49 ($\pm$ 0.11 SD, n = 28) in temperate forests. Vicca *et al.* (16) postulated that this large

158   difference in NPP/GPP between boreal and temperate forests is mainly due to the

159   typically higher fertility in temperate forests, where trees invest less photosynthates in

160   nutrient acquisition mechanisms such as exudation or symbionts, leaving a higher

161   fraction of GPP available for wood production.

162   Within both the boreal and temperate biomes, we observed a stable NPP/GPP

163   ratio across age (Fig. 4). Paired GPP-NPP data indicate that the correlation between

164   GPP/NPP and age is not significant (slope $p > 0.05$) in both temperate and boreal forests.

165   This constancy with age (two black lines in Fig. 4) contradicts with the original theorem,

166   where the NPP/GPP ratio is expected to decrease with age because NPP declines and

167   GPP stabilizes (the grey line in Fig. 4). Our observed trend of insensitivity of NPP/GPP

168   to age within a biome but significant difference between boreal and temperate forests

169   disagrees with previous publications that NPP/GPP decreases with age (23, 24). We also

170   disagree with that NPP/GPP tends to be conservative across age classes and ecosystems

171   (25-28) and agrees with the variability of NPP/GPP across ecosystems (23). Recent

172   studies has shown that the NPP/GPP ratio could by influenced more by temperature (29)

173   or by nutrient availability (16) than by age.

174   In the classical model, R_a would be expected to continue to increase as forests age

175   (Fig 1). Both our calculated R_a lines and measurement data contradict this classical

176   hypothesis, with a decrease in R_a after maturity (Fig. 3), in agreement with findings of

177   Ryan et al. (2, 3, 10). The primary explanation for the hypothesized continuous increase

178   in respiration was that, while leaf respiration stabilizes with maximum leaf area index

179   after canopy closure, wood respiration continues to increase with the accumulation of

180   woody biomass in ageing forests (9). In recent years, many studies have indicated the

181   tight coupling between ecosystem GPP and respiration (30-33), which is not surprising

182   given that plants cannot respire more than the available supply of recent or stored

183   photosynthate. This tight coupling between GPP and respiration not only substantiates the

184   indication for a constant NPP/GPP ratio with age within a biome, but also suggests that

185   the decrease in GPP is the prime reason for the decline in R_a. If the respiratory carbon

186   cost is indeed a fixed proportion of GPP, then a reduction in GPP with age would be the

187   main cause of the widely observed age-driven decline in NPP.

188   There are other mechanisms that uncouple respiration from accumulated biomass

189   stocks in ageing forests and could explain the reduction in R_a more mechanistically. If

190   autotrophic respiration is partitioned into growth and maintenance respiration, the latter

191   may increase with age due to the increase in standing biomass, but growth respiration

192   would decline with the age-related decrease in NPP, perhaps offsetting the increase in

193   maintenance respiration, and thus potentially resulting in a decrease in total autotrophic

194   respiration (2). Moreover, leaf and root biomass are unlikely to increase with ageing, and

195   the respiratory sapwood only accounts for a small fraction of the accumulated woody

196   biomass in ageing forests. Hence, any age-related increase in maintenance respiration

197   with increasing forest age is expected to be very limited. An empirical study has indeed

198   shown that stem respiration in an old-growth hardwood stand decreased compared with

199   young and mature stands in the Great Lakes area (13).

200   Because our results for age-related trends in GPP and R_a for both boreal and

201   temperate forests oppose the traditional view of the mechanism underlying the age-

202   related decline in forest NPP, we propose here a new conceptual model (Fig. 5). This

203   conceptual model, presented in terms of parameterized Γ functions, builds on that

204   proposed earlier by Ryan et al. (2), but differs from both the classical model and this

205   newer view in that we specify that the decrease in NPP results from the combined effects

206   of (A) a decline in GPP with increasing age and (B) an approximately constant NPP/GPP

207   ratio independent of age, i.e., R_a follows the change in GPP but decreases more slowly

208   with increasing age than GPP in ageing forests. Our results suggest that the age effect on

209   forest GPP, R_a and NPP, independent of climatic and edaphic controls and management

210   practices, is of fundamental importance for understanding patterns of forest growth and

211   carbon dynamics. Long-term forest ecosystem models must therefore also consider age as

212   a dominant control on spatial and temporal patterns of forest productivity in order to

213   realistically simulate carbon cycles. The ratio of NPP/GPP (and thus of R_a/GPP), is

214   highly variable across biomes, but appears independent of age in mature forests within a

215   biome. The decline in NPP in ageing forests is mainly driven by the reduction in GPP.

216   The mechanism of reduced GPP with age needs further studies.

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218   **Materials and Methods**

219   We used an established global database (15) of forest GPP and NPP, obtained

220   from eddy covariance measurement (34, 35), chamber-based flux measurement,

221   biometric inventories, modeling results, and corresponding site properties and climatic

222   parameters to investigate the age effect on GPP, NPP, R_a and NPP/GPP. The database

223   was assembled from published literature, existing computer databases (36, 37), and the

224   AmeriFlux and CarboEurope networks within the FLUXNET (38). NPP was typically

225   measured by the sum of incremental biomass of forest woods and annual production of

226   leaves and roots. Estimating NPP for roots is challenging (39) and allometric equations

227   (e.g. 6), root in-growth cores (40), or minirhizotrons (e.g. 41) are often used. GPP was

228   derived from eddy covariance measurements (34, 35), modeling results, or biometric (for

229   NPP) plus chamber measurement (for R_a). Chamber-based measurement of R_a is the sum

230   of respiration from individual components (woods, leaves, and roots) (e.g. 13).

231   We compiled a subset of the database by using only annual sums of GPP, NPP, R_a,

232   and age (years since regeneration after a major disturbance, e.g., harvest, fire, or land-use

233   shift). We excluded any forest sites subject to major experimental or management

234   treatments (e.g. elevated ambient CO_2 concentration, fertilization, thinning, and/or

235   irrigation). We also averaged multiple years, where available, of GPP, NPP, and R_a to

236   obtain mean annual values. For those sites with different GPP values originating from

237   multiple methods, we used only eddy covariance derived GPP. Though reporting

238   uncertainty is important (42), most individual datasets do not contain uncertainty levels.

239   Based on the literature reports on eddy flux uncertainty (14, 43) and expert judgment (15),

240   the uncertainty, varying among individual sites, was less than 30% for GPP and 20% for

241   NPP for our dataset. We have not found any evidence that the uncertainty is correlated

242   with forest age. We also acknowledge the uncertainty associated with the chronosequence

243   approach (e.g. 5) that we used to study the age effect on GPP, NPP, and R_a, given the

244   variability of site conditions. Therefore, we grouped datasets by major biomes and

245   assumed that this uncertainty associated with the chronosequence method is randomly

246   distributed within a biome.

247   We categorized all forest sites into boreal, temperate, Mediterranean, and tropical

248   biomes based on climatic characteristics and species mixtures. Due to limited

249   measurement data in Mediterranean and tropical sites for regression analysis, in this

250   study we only analyzed boreal and temperate sites. As a result, we obtained 73 sites with

251   GPP data, 166 sites with NPP data, 17 sites with independently measured R_a data (not

252   calculated from GPP - NPP), and 45 paired GPP-NPP datasets all accompanied with age

253   data (See Supporting Information for details). Paired GPP-NPP data mean that both GPP

254   and NPP were independently measured at one site at the same or close to the same year

255   so that we could directly calculate the NPP/GPP ratio for this site.

256   We used a gamma (Γ) function (Eq. 1) to fit the age effect of GPP and NPP for

257   both boreal and temperate biomes. This type of function has been used to describe the

258   age-driven change of forest floor organic matter (44) even though the simplicity of the

259   pattern has been challenged by field-based data (45).

260    $$y = k_0 t^{k_1} e^{k_2 t} \ , \qquad\qquad \text{(Eq. 1)}$$

261   where y is GPP or NPP (g C m^{-2} y^{-1}), t is the forest age (in years since the last major

262   disturbance such as harvest or fire), and k_0, k_1, and k_2 are parameters.

263   Equation 1 could be log-transformed to a linear equation. Parameters in Eq. 1

264   were then estimated by conducting multivariate linear regression. Two sets of the Γ

265   function for GPP and NPP, respectively, allowed us to analytically derive R_a (GPP – NPP)

266   and the ratio of NPP/GPP as a function of age. Independently measured NPP/GPP and R_a

267   data were used to validate the modeled results of NPP/GPP and R_a.

268   We determined the age at which maximum values of GPP and NPP were obtained

269   by differentiating Eq. 1. (Eq. 2).

270         $$y_{max} = k_0(-k_1 / k_2)^{k_1} e^{-k_1}, \text{ when } t = -k_1 / k_2. \qquad \text{(Eq. 2)}$$

271   We also tested different functions to fit the data, including a second-degree

272   polynomial function, a third-degree polynomial function, a logarithm function, and a

273   Michaelis-Menten function ($y = ax/(b + x)$). We used the root mean squared error (RMSE)

274   to evaluate the model accuracy and efficiency. We also used the Akaike Information

275   Criterion (AIC) to compare models as AIC considers both the lowest RMSE and the

276   fewest model parameters, accounting for both goodness-of-fit and the complexity of the

277   model (46, 47). When the number of parameters (p) is large comparing with the sample

278   size (n) (generally $n/p < 40$), we used AIC$_c$ (Eq. 3) (47). The model with the lowest AIC$_c$

279   is the best candidate.

280         $$AIC_c = n\log\sigma^2 + 2p + \frac{2p(p+1)}{n-p-1}, \qquad \text{(Eq. 3)}$$

281   where n is the number of observations, σ is the RMSE, and p is the number of parameters.

282   Because the age data are not evenly distributed with less data in older forests, we

283   used the "Cook's Distance" to estimate the influence of a data point (48), for example, in

284   old-growth forests:

285    $$D_i = \frac{\sum_{j=1}^{n}(\hat{Y_J} - \widehat{Y_{J(\iota)}})^2}{p\,(MSE)}\,,$$ (Eq. 4)

286   where D_i is the Cook's Distance for data point i, $\hat{Y}_j$ is the predicted value from the model

287   for data point j, $\hat{Y}_{j(i)}$ is the predicted value for point j from the model in which point i has

288   been omitted, p is the number of fitted parameters in the model, and MSE is the mean

289   square error (deviation), or $RMSE^2$. The Cook's Distance considers both the x value and

290   y value to evaluate if a data point is highly influential (an outlier). Though controversial,

291   The point with $D_i > 1$ is considered a highly influential point (49). If there are points with

292   substantially high D_i than others, we carefully re-check the points by comparing

293   regression with and without these points and remove the points if they are outliers.

294   Statistical analyses were conducted with the statistical package Stata (Stata

295   Corporation, Texas, USA).

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Figure legends

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447   Fig. 1 The traditional conceptual model of GPP, NPP, and R_a as a function of forest age

448   (modified from Kira and Shidei (9) and Odum (10)). The grey area indicates NPP, the

449   difference between the GPP line and R_a line.

450

451   Fig. 2 The NPP patterns with forest age in boreal (A) and temperate (B) forests. The dots

452   are NPP measurements. The solid lines are fitted from measurement data (Eq. 1, Table 1).

453   The grey shades indicate 95% confidence interval of fitted NPP.

454

455   Fig. 3 The GPP and R_a patterns with forest age in boreal (A) and temperate (B) forests.

456   The dots are measurement data. The solid lines indicate the modeled GPP using Eq. 1 and

457   parameters from Table 1. The dash lines indicate the calculated R_a as GPP – NPP.

458

459   Fig. 4 Changes in NPP/GPP with age in boreal and temperate forests. The dots are

460   measurements from paired GPP-NPP data. The black lines are derived from the modeled

461   GPP and NPP using Eq. 1 and parameters from Table 1. The grey line is conceptual

462   following Odum's traditional model in Fig. 1.

463

464   Fig. 5 Our new model showing the decrease in NPP resulting from both decreases in GPP

465   and R_a in boreal (A) and temperate (B) forests, in contrast to Fig. 1. The GPP line and the

466   grey area of NPP are fitted from measurement data (Eq. 1, Table 1), and the R_a line is

467   derived from fitted GPP and NPP as GPP – NPP.

A. Boreal

B. Temperate

Age (year)

Legend:
- Boreal modeled (solid line)
- Boreal measured (filled circle)
- Temperate modeled (dashed line)
- Temperate measured (open circle)
- Odum's NPP/GPP (gray line)

Y-axis: NPP/GPP (0.0 to 0.8)
X-axis: Age (year) (0 to 500)

A. Boreal — Carbon flux (g C m^{-2} y^{-1}) vs Age (year); NPP, GPP, R$_a$.

B. Temperate — Carbon flux (g C m^{-2} y^{-1}) vs Age (year); NPP, GPP, R$_a$.