Plant respiration: controlled by photosynthesis or biomass?

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Abstract

Two simplifying hypotheses have been proposed for whole-plant respiration. One links respiration to photosynthesis; the other to biomass. Using a first-principles carbon balance model with a prescribed live woody biomass turnover, we show that if turnover is fast, the accumulation of respiring biomass is low and respiration depends primarily on photosynthesis; while if turnover is slow, the accumulation of respiring biomass is high and respiration depends primarily on biomass. But the first scenario is inconsistent with evidence for substantial carryover of fixed carbon between years, while the second implies far too great an increase in respiration during stand development – leading to depleted carbohydrate reserves and an unrealistically high mortality risk. These two mutually incompatible hypotheses are thus both incorrect. Respiration is *not* linearly related either to photosynthesis or to biomass, but rather it is more strongly controlled by recent photosynthates (and reserve availability) than by total biomass.

INTRODUCTION

The amount of carbon that accumulates in actively growing stands of vegetation depends on the balance of photosynthesis (gross primary production, P) and whole-plant respiration (R). The difference between these fluxes is net primary production (P_n). Most annual P_n is allocated to structural growth (G), but some is stored as non-structural carbohydrates (NSC, mostly starch and sugars), some is released back to the atmosphere in the form of biogenic volatile organic compounds (BVOCs), and some is exuded to the rhizosphere (Chapin *et al.* 2006). The fraction of P that accumulates in biomass, and the fraction that returns to the atmosphere through plant metabolism, are crucial quantities that determine the sign and magnitude of the global climate-carbon feedback – which remains one of the greatest sources of uncertainty in the global carbon cycle (Friedlingstein *et al.* 2014). But despite many ecophysiological studies aiming to understand P_n and R dynamics during stand development a general understanding is still lacking.

Some authors have hypothesized a constant P_n:P (carbon use efficiency, equivalent to 1 – (R:P)) ratio, with R tightly constrained by P irrespective of biomass, climate, tree species and stand age (e.g. Gifford 2003; Van Oijen *et al.* 2010). Waring *et al*. (1998, W98 hereafter) indicated a universal P_n:P of ~ 0.5. Since R depends on the matter produced by photosynthesis, Gifford (2003) suggested that these two processes must be balanced over the longer term – making R proportional to P, consistent with W98. He argued that prescribing P_n (or R) as a constant fraction of P could be a simpler, and potentially more accurate, alternative to explicit, process-based modelling of R. A number of land vegetation models (reviewed in Collalti & Prentice 2019) have adopted this simplification.

An alternative hypothesis, grounded in metabolic scaling theory, suggests that R should scale with biomass following a power law, $Y = a\,X^b$ (West *et al*. 1999). According to some studies (e.g. Reich *et al*. 2006, R06 hereafter), R (Y) scales isometrically (b ~ 1) with whole-plant carbon (C) or nitrogen (N) contents (X), and this scaling is similar within and among different species, and irrespective of environmental and climatic conditions – which might influence the

normalization constant (a), but not the exponent (b). Isometric scaling of R with biomass was assumed in the traditional view of forest dynamics set out e.g. by Kira & Shidei (1967) and Odum (1969). In the absence of major disturbances, if R increases in parallel with biomass, then P_n necessarily declines – because P cannot increase indefinitely, but rather stabilizes at canopy closure. Mori *et al*. (2010) however indicated that biomass and R are isometrically related only in young trees, tending towards $b \sim {}^3/_4$ in mature trees. A general value of ${}^3/_5$ has also been proposed (Michaletz *et al*. 2014). But however it is interpreted, this scaling hypothesis implies that R depends on biomass, and is related to P only to the extent that P and biomass vary together.

Many terrestrial biosphere models simulate plants respiration more explicitly, thus partially uncoupling R from P. The most widely used (and observationally supported) method, also adopted here, divides R into growth (R_G) and maintenance (R_M) components (McCree 1970). R_G is considered to be a fixed fraction of new tissue growth, independent of temperature, the fraction varying only with the cost of building the compounds constituting the new tissue (Penning de Vries 1972). Temperature, substrate availability and the demand for respiratory products are considered to control R_M (Cannell & Thornley 2000). Several studies have investigated the effects of short- and long-term changes in temperature on R_M, mostly at the leaf level (e.g. Heskel *et al.* 2016; Huntingford *et al.* 2017). The nature of the temperature responses and the acclimation of R_M are important and much-discussed issues, but they are not considered further here. In contrast, the effects on respiration of woody biomass (the substrate), its accumulation, and the transition rate of respiring sapwood into non-respiring heartwood, have received relatively little attention (Tjoelker *et al.* 1999; Kuptz *et al.* 2011). These latter processes are the focus of this review.

The fixed-ratio hypothesis of W98 and the scaling hypothesis of R06 could both be used – at least in principle, across the twenty orders of magnitude variation in plant mass – to estimate R and P_n without the need for explicit process-based modelling of R (McMurtrie *et al.* 2008; Price

et al. 2010). However, they yield quite different results, and both hypotheses have been subject to criticism (e.g. Medlyn & Dewar 1999; Mäkelä & Valentine 2001; Kozłowski & Konarzewski 2005; O'Connor *et al*. 2007; Keith *et al*. 2010; Agutter & Tuszynski 2011; Price *et al.* 2012; Collalti *et al*. 2018; Collalti & Prentice 2019). To our knowledge, there has been no previous attempt to compare these hypotheses directly, and their consequences for forest carbon balance during stand development, in a consistent modelling framework. We attempt to fill this gap by providing illustrative simulations of the long term trajectories of R, P_n and P_n:P. The simulations are based on the first principles of mass balance implemented in a process-based, ecophysiological model that has been tested against detailed time-series observations in a real forest stand. Our aim is to provide insight into the consequences of different assumptions about live woody biomass turnover (live woody biomass is the metabolically active fraction of sapwood: see Supporting Information). We show how different (extreme) assumptions about the live woody turnover map on to the alternative hypotheses, while seeking an answer to the pivotal question: is R a function of photosynthesis alone (W98), or of biomass alone (R06)? Or are neither correct?.

METHODS

Theoretical framework

A general equation describing autotrophic respiration (R) is:

$$R = P - P_n = P - (G + G_{\mathrm{R}}) \quad (1)$$

where P and P_n are gross and net primary production, G is structural and litter biomass production and G_R is the flux to NSC reserves and secondary compounds including, exudates and BVOCs (all in g C ground area^{-1} time^{-1}). If R is further decomposed into growth (R_G) and maintenance (R_M) respiration (McCree 1970), then:

$$R = R_{\mathrm{G}} + R_{\mathrm{M}} = g_{\mathrm{R}}\mathrm{G} + m_{\mathrm{R}}W_{live} \quad (2)$$

where g_{R} and m_{R} are the growth and maintenance respiration coefficients (i.e. respiratory CO_2 released per unit biomass produced by growth and by the maintenance of the existing biomass: both, per unit time and unit mass), and W_{live} is living biomass (Amthor 2000). W_{live} can be broken down further:

$$W_{\mathrm{live}} = W_{\mathrm{live_woody}} + W_{\mathrm{green}} \quad (3)$$

where $W_{\mathrm{live_woody}}$ and W_{green} are the biomass of live woody pools (living cells in stem, branches and coarse roots) and non-woody tissues (leaves and fine roots), respectively. Because plant tissues require N as a component of the enzymes that sustain metabolic processes, living biomass is often expressed in nitrogen units, g N ground area^{-1} (Cannell & Thornley 2000), while respiration is expressed in carbon units. Then m_{R} is in units of g C g N^{-1} time^{-1}. Temporal changes in $W_{\mathrm{live_woody}}$ can be summarized by first-order biochemical kinetics:

$$\underbrace{\frac{\mathrm{d}W_{\mathrm{live_woody}}}{\mathrm{d}t}}_{\text{relative change}} = \underbrace{\varphi \cdot G_{\mathrm{live_woody}}}_{\text{incoming flux}} - \underbrace{W_{\mathrm{live_woody}} \cdot \tau}_{\text{outgoing flux}} \quad (4)$$

where $G_{\mathrm{live_woody}}$ is the part of G allocated to live woody, φ converts carbon to nitrogen content (g N g C^{-1}), and τ is the live woody turnover rate per unit time (t). A similar expression can be written for W_{green}. The first term on the right-hand side of equation (4) represents the "incoming" flux of new living cells; while second term represents the "outgoing" flux of living cells that die and become metabolically inactive. But while W_{green} may be only a small fraction of total forest biomass, not changing much after canopy closure, $W_{\mathrm{live_woody}}$ (as also total W) becomes large during forest development and is potentially a strong driver of R (Reich *et al.*

2008). Note that this general approach including a turnover rate parameter (τ) is equally valid for any mass-, area- or volume-based analyses (Thornley & Cannell 2000).

Setting τ = 1 year^{-1} in equation (4) would imply a tight coupling between the previous year's growth and the current year's respiration flux – as suggested by Gifford (2003) – and yields a close approximation to the W98 assumption of a fixed ratio between P_n and P, thus cancelling any effect of biomass accumulation. The implication of a one-year-lag between carbon fixation and respiration in woody compounds is consistent with the findings of Amthor (2000), Kagawa *et al*. (2006a, b), Gough *et al*. (2008, 2009) and Richardson *et al*. (2013, 2015) of a physiological asynchrony by about one year between P.

Alternatively, setting τ = 0.1 year^{-1} would imply that most new sapwood cells live for many years, and would closely approximate the R06 assumption of proportionality between R and biomass. Thus, the amount of respiring biomass is regulated by the amount of substrate that is produced each year, forming new sapwood, versus the amount that is converted into non-living tissues and no longer involved in metabolism; the balance of these processes being controlled by τ (see proofs-of-concept in Fig. 1a and b, and Table 1 for elaboration).

Because carbon supply (photosynthesis) and carbon metabolic demand (respiration) are not necessarily synchronized, the model assumes that temporary carbon imbalances between P and R (implying $P_n < 0$, Roxburgh *et al.* 2005) are met by the remobilization or recycling of NSC stored during previous year(s) – so long as the NSC pool is not completely emptied (the carbon starvation hypothesis; McDowell *et al.* 2008). A full description of the modelled NSC dynamics is provided in Box 1.

Simulation set-up

The logic described above was implemented in the process-based forest growth model 3D-CMCC-CNR and applied, as a case study, to a temperate deciduous forest. Additional model

description can be found in Supporting Information, Collalti *et al*. (2014, 2016, 2018), and Marconi *et al*. (2017).

Very limited data are available on the turnover rate τ of live cells in sapwood, which is often either guessed or inferred by model calibration (e.g. White *et al.* 2000). We carried out ten simulations with τ varied in arbitrary 0.1 yr^{-1} steps, from τ = 1 yr^{-1} (100% of turnover, all the previous year live cells of sapwood becomes non-respiring heartwood in the current year), down to τ = 0.1 yr^{-1} (only 10% of the previous year's live cells of sapwood biomass dies). Thus, we started with the largest prior distribution for τ, assuming that values outside this range are not functionally possible (Table 1). We are unaware of any studies reporting changes in τ with age or biomass; we have therefore assumed that τ is constant in time.

The standard configuration of 3D-CMCC-CNR assigns τ = 0.7 yr^{-1} (Collalti *et al.* 2019) and this same value has been used by several authors in various modelling contexts (e.g. Bond-Lamberty *et al.* 2005; Tatarinov & Cenciala 2006). Other models have applied different values (see Box 2). Zaehle *et al*. (2005), Poulter *et al.* (2010) and Pappas *et al*. (2013) found that τ is a critical parameter for both LPJ-DGVM and LPJ-GUESS. We are not aware of similar sensitivity analyses for other models. Leaf and fine root turnover rates are assumed here to be 1 yr^{-1}, appropriately for deciduous trees (Pietsch *et al*. 2005). The model parameter for maximum age (a parameter that controls, among other things, an age-effect on leaf conductance: Kirschbaum, 2000; Smith *et al.* 2001) was set arbitrarily large, to avoid building in prior assumptions about age effects. Age- and size-effects are therefore considered synonymous (Mencuccini *et al.* 2005). A stochastic background whole-tree mortality rate (1% of trees removed each year) was retained and included in equation (4) to ensure a realistic self-thinning (Smith *et al.* 2001; Kirschbaum, 2005). All other parameters were left unchanged from the standard model configuration.

Test site and model run

The model was applied to simulate the development of an even-aged stand of European beech (*Fagus sylvatica* L.; Sorø, Denmark; Wu *et al.* 2013, Reyer *et al.* 2019: http://doi.org/10.5880/PIK.2019.008) in daily time steps from 1950 to 2100. The reasons for choosing this stand are: (a) the extensive literature on European beech, allowing key parameter values to be assigned with confidence; (b) the exceptional quantity of data available at the Sorø site for initializing and evaluating the model; and (c) because the trees are deciduous we can assume a complete annual turnover of leaves and fine roots and, therefore, more easily disentangle the contributions of W_{green} and $W_{\mathrm{live_woody}}$. Deciduous species are also expected to have greater within-season variability in P_n:P, and greater asynchrony in carbon supply and demand, than evergreen species (Dietze *et al*. 2014; Martínez-Vilalta *et al*. 2016). However, the model results are based on general principles and expected to apply more generally.

We simulated forest development up to 2100, consistent with the common economic rotation length for this species in northern Europe. After canopy closure, modelled leaf area index (LAI) and the relative amounts of leaf and fine-root biomass became stable or even slightly decrease, as is usually observed (Yang *et al.* 2011, 2016). Therefore, changes in modeled R and its components R_{M} and R_{G}, could be attributed to changes in the total amount of living woody biomass and the costs of its maintenance.

In 1950 the stand was aged 30 years with an average tree diameter at breast height of ~ 6 cm and a density of 1326 trees ha^{-1}. Model state variables were initialized using species-specific functional and allometric-relationships from the literature, and previous model applications at this site (Collalti *et al.* 2016, 2018; Marconi *et al.* 2017). Model sensitivity to parameter values and their uncertainties have been assessed in depth in a previous work (see Collalti *et al.* 2019, especially their Fig. 2 and Table 3). Management, in the form of thinning, occurred at the site only up to 2014. After that year, only stochastic mortality was accounted for in the model. Live

wood was initialized at 15% of sapwood biomass (as the fraction of current year sapwood: Pietsch *et al.* 2005) and assigned a C:N ratio of 48 g C g N^{-1}, not changing with increasing biomass (Ceschia *et al.* 2002; Damesin 2003). The minimum concentration of NSC was assumed to be 11% of sapwood dry mass (Hoch *et al.* 2003; Genet *et al.* 2010; Martínez-Vilalta *et al.* 2016). Daily meteorological forcing variables were obtained as historical ensemble means from five Earth System Models up to 2005 provided by the Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP, Warszawski *et al.* 2014). Data for the period 1995–2005 were then randomly repeated up to 2100. Additional simplifying assumptions were made in order to focus specifically on the effects of increases in tree size, as follows: no disturbances (whether herbivory or management) after 2014; no effect of changes in soil N availability; and, importantly, to avoid possible confounding of temperature effects on R_M with other warming effects, a stable (1995–2005) climate and atmospheric CO_2 concentration (~ 380 μmol mol^{-1}). Exports of carbon to exudates and BVOCs were neglected.

RESULTS

Data-model agreement

The standard model configuration satisfactorily reproduced P, R, P_n and the ratio P_n:P when compared to independent, site-level, carbon balance data (Wu *et al.* 2013) for the period 2006–2010 (Fig. 2, Table 2), corresponding to a stand age of ~ 85–90 yrs. P was in agreement with eddy covariance data, while R was slightly underestimated compared to values in Wu *et al.* Consequently, the model overestimated the average P_n:P ratio by 14% compared to Wu *et al.* However, Wu *et al.* argued that the values of R they obtained (by subtracting modelled heterotrophic from measured ecosystem respiration) may have been somewhat overestimated, given also the ample standard deviation (±143 g C m^{-2} yr^{-1}). The model results are otherwise in good agreement with Wu *et al.* for woody carbon stocks (both above- and below-ground), annual wood production (the sum of carbon allocated to stems, branches and coarse roots), and annual

above- and below-ground litter production (the sum of carbon allocated to leaves and fine roots) (Table 2). Modelled respiration of the woody compartments, leaf and total (above- and below-ground) respiration, and NSC pool and fluxes, are all compatible with values reported by previous investigations, and within the ranges of total, wood and leaf respiration, and P_n:P ratios reported for European beech (e.g. Barbaroux & Brèda 2002; Barbaroux *et al.* 2002; Knohl *et al.* 2003; Granier *et al.* 2008; Davi *et al.* 2009; Genet *et al.* 2010; Guidolotti *et al.* 2013). A model validation forced by measured climate at this site is also described in previous papers (Collalti *et al.* 2016; 2018; Marconi *et al.* 2017).

The effect of varying τ

The simulations produced a broad spectrum of diverging trajectories, ranging from an approximately constant P_n:P ratio (for large τ) to a constantly decreasing P_n:P ratio (for small τ) (Fig. 1a). For τ = 1 yr^{-1}, P_n:P stays close to 0.5. For $\tau \leq 0.2$ yr^{-1} P_n:P eventually falls below the lower limit of commonly observed values (0.22; Collalti & Prentice 2019) and the physiological limit of 0.2 proposed by Amthor (2000). Figure 2 also shows the effects of varying τ in determining different trajectories for P_n (Fig. 2b) and R (Fig. 2c) and consequent differences in the partitioning between R_M and R_G (Fig. S2) with modelled R, at the end of simulations, ranging from ~ 800 g C m^{-2} yr^{-1}, giving P_n ~ 900 g C m^{-2} yr^{-1} and P ~ 1700 g C m^{-2} yr^{-1} (Fig. S1 and for NSC flux Fig. S3b) consistent with a steady-state between R or P_n and P, to two cases (τ = 0.1, 0.2 yr^{-1}) in which trees die from starvation.

The model did not generate any consistent power-law relationship between R and biomass either for b ~ 1 (i.e. R06), or for ~ $^3/_4$ (Mori *et al.* 2010), or for ~ $^2/_3$ (Makarieva *et al.* 2005), and for ~ $^3/_5$ (Michaletz *et al.* 2014) (Table S1). The simulations indicated b ~ 1 initially, shifting with increasing tree size to b ~ 0.74 for τ = 0.1 yr^{-1} (R^2 = 0.99, n = 117) or 0.19 for τ = 1 yr^{-1} (R^2 = 0.84, n = 150; 'n' corresponds to years of simulation). For the relation between R and whole-plant N, again the simulations indicated b ~ 1 initially, shifting to b ~ 0.82 for τ = 0.1 yr^{-1}

(R^2 = 0.99, n = 117) or 0.27 for τ = 1 yr^{-1} (R^2 = 0.82, n = 150) (Figs. 3a and 3c). Note that the highest b values corresponded to simulations which ended because the trees died.

DISCUSSION

R is not entirely determined by P

A constant P_n:P ratio, obtained on the model by setting τ = 1 yr^{-1}, conflicts with observations that show a substantially slower turnover rate of living cells. Parenchyma cells within secondary xylem are very often more than a year old, and can be up to 200 years old (Spicer & Holbrook 2007). The constant ratio hypothesis is also contrary to the evidence that much of the recently-fixed assimilate pool is at first stored as reserves, and only later used for metabolism or growth (Schiestl-Aalto *et al.* 2015, 2019). Indeed, some report decoupling between growth (which would imply some CO_2 released for both R_G and subsequently R_M) and photosynthesis – with growth ceasing long before photosynthesis – because of their different sensitivities to environmental drivers. Kagawa *et al*. (2006a) reported that up to 43%, and according to Gough *et al*. (2009) up to 66%, of annual photosynthetates are used during the year(s) after they have been fixed. Gaudinski *et al*. (2009), Malhi (2012), and Delpierre *et al*. (2016) all found negative correlations between annual carbon inflows and above- or below-ground wood growth. Chen *et al*. (2013) found that R does not scale isometrically with P. Some suggested that R_G could be supplied exclusively by recent photosynthates while R_M by the previously stored ones (L□tscher *et al*. 2004). Along the same lines, Maier *et al*. (2010), Kuptz *et al*. (2011) and Lynch *et al*. (2013) found that both R_G and R_M are not completely satisfied by recent assimilates, and that some current R_M can be derived from woody tissues constructed in previous years. Litton *et al*. (2007) and Yang *et al*. (2016) both found low correlations between respiration and the annual production of woody compounds. Many studies have also reported little variation in the CO_2 efflux from sapwood in relation to tree-ring age, despite a stepwise decrease in the fraction of living cells towards the centre of the stems (e.g. Ceschia *et al.* 2002; Spicer & Holbrook 2007;

Pallardy 2010). These various observations imply that some carbon is fixed one year and used for the tree's own growth and metabolism in the next or subsequent years, and that the inner sapwood contains a population of living cells formed in previous years.

These observations are all incompatible with the hypothesis of a tight coupling of R and P (alone), and with model results obtained by assuming complete turnover of live cells in sapwood during a single year.

R is not entirely determined by biomass

On the other side of the ledger, model simulations indicate that low τ values (≤ 0.2 yr^{-1}) can lead to excessively high respiration burdens, impossibly low P_n:P ratios (< 0.2), and ultimately carbon starvation when all NSC is consumed and whole-tree R_M or growth can no longer be sustained (Fig. 2). This model result is quantitatively dependent on the values adopted for C:N ratio and the minimum NSC-pool which increases with tree size, but is consistent with the idea that P_n:P ratios ≤ 0.2 are not physiologically sustainable (Amthor, 2000). Amthor described the 0.65–0.2 bounds as those reflecting maximum-growth with minimum-maintenance expenditure (0.65) and minimum-growth with maximum physiologically-sustainable maintenance costs (0.2). Such a minimum P_n:P value agrees also with Keith *et al.*'s (2010) considerations that trees require always some annual biomass (litter) production in order to survive. With such low τ, simulated woody R_M:$R > 90\%$, a value much higher than those (56–65%) reported by Amthor & Baldocchi (2001) (Supporting Information Fig. S2), and this initiates a spiral of decline, whereby neither P nor NSC drawdown are sufficient to avoid a long term carbon imbalance (Supporting Information, Figs. S3a and b; Wiley *et al.* 2017; Weber *et al.* 2018).

Slightly higher τ values (from 0.3 to 0.5 yr^{-1}) were found to limit woody biomass increase because of high NSC demand, leading to a shift in the allocation of assimilates to refill NSC at the expense of growth, and P_n:P values close to 0.2 (Fig. 2a). Values of $\tau > 0.5$ did not show such behaviour and allowed structural and non-structural compounds to accumulate in parallel,

while P_n gradually declined and eventually levelled off. This scenario allows structural biomass accumulation to continue even in older trees, as observed (Stephenson *et al*. 2014).

Scaling relationships

We simulated forest dynamics from juvenile up to very large, mature trees. R06's results supporting isometric scaling were based on measurements of seedlings and 6- to 25-year-old trees with, presumably, very little heartwood. Mori *et al*. (2010) analysed single trees located outside forests, so neither of these studies is strictly comparable with ours. Some other studies have suggested that the scaling slope of approximately 1 for whole-plant mass may be valid early in stand development, but that the exponent may eventually become smaller than $^3/_4$, a phenomenon that has been termed 'ontogenic drift' (Makarieva *et al.* 2008). Piao *et al.* (2010) in a global analysis also found a low correlation, and a low scaling exponent, between R and whole-plant biomass ($b \sim 0.21$, corresponding to $\tau \sim 0.9$ in our simulations). Piao *et al*. (2010) argued that, for large mature trees, an increasing fraction of woody C and N biomass is composed of metabolically inactive heartwood, and concluded that a linear-relationship between respiration and whole-plant biomass should not be expected, while a curvilinear-relationship at the small end of the size spectrum seemed more appropriate (Kozłowski & Konarzewski 2005). Li *et al*. (2005) also found no evidence for an isometric or $^3/_4$ power scaling relationship, indicating instead a range between 1.14 and 0.40, decreasing with plant size. The only approximately isometric relationship we found in our simulations – across all τ used – was between R and the living components of biomass C (b in the range of 0.8 to 1, with R^2 always > 0.93) and biomass N ($b \sim 0.9$, with R^2 always > 0.97) (Figs. 3b and 3d; Makarieva *et al*. 2005; Kerkhoff & Enquist 2006; Gruber *et al.* 2009).

Overall, none of these findings are compatible with a tight isometric-relationship of R to whole-plant C (or N) biomass and model results lend mechanistic support to this view.

R is determined by P, biomass and reserve availability

Plants store large amounts of non-structural carbohydrates (e.g. up to rebuild the whole leaf canopy one to more than four times, Hoch *et al*. 2003) and, when need, plants can actively buffer the asynchronies between carbon demand (i.e. *R* and *G*) and supply (i.e. *P*) by tapping the pool of non-structural carbon resources (see Fig. S3 in Supporting Information for NSC trends). Several lines of evidence and a growing body of literature support the view of a (at least) quasi-active sink of NSC, that is, NSC competes with growth, while it controls *R* (and including other nonmetabolic functions, see Hartmann & Trumbore 2016), in a feed-forward circular mechanism. Schuur & Trumbore (2006), Carbone *et al*. (2007) and Lynch *et al*. (2013) all reported that plant-respired CO_2 is a mixture of old and new assimilated carbohydrates. Likewise, Vargas *et al*. (2009), Carbone *et al*. (2013), Richardson *et al*. (2013); Muhr *et al*. (2013, 2016), and Solly *et al.* (2018) found that NSC up to 17 year old, remobilized from parenchyma cells, can be used for growth or metabolism.

Aubrey & Teskey (2018) found that carbon-starved roots and whole-tree saplings die before complete NSC depletion, but the threshold NSC level at which this happens remains largely unknown or uncertain for most species. These thresholds are likely to vary among tissues (Weber *et al.* 2018), species (Hoch *et al.* 2003), phenotypes, habit and wood anatomy (Dietze *et al.* 2014), and to increase with tree size (Sala *et al.* 2012). Others have reported that trees cannot draw down NSC to zero because of limitations in carbohydrate remobilization and/or transport (Hartmann & Trumbore 2016; Wiley *et al.* 2017). A minimum NSC level, which has been found to proportionally increase with size biomass, may also be required to maintain a safety margin and a proper internal functioning of trees (e.g. osmoregulation), regardless of whether growth is limited by carbon supply (Woodruff & Meinzer 2011; Sala *et al*. 2011, 2012; Martínez-Vilalta *et al*. 2016; Huang *et al.* 2019). Genet *et al*. (2010) found shifts during ontogeny in carbon allocation from biomass growth to reserves regardless of seasonal fluctuations, habitat and

climate and Palacio *et al*. (2012) found that in repeatedly defoliated trees for 11 yrs, and left to recover for other 6 yrs, reduced growth but similar stem NSC concentration when compared to other undefoliated trees.

It has further been suggested that a considerable fraction of NSC (mostly starch) in the inner-part of wood may become compartmentalized and sequestered away from sites of phloem loading, and thus no longer accessible for both tissue-growth and respiration (Sala *et al.* 2012). Root exudation to mycorrhizal fungi and secondary metabolites (not accounted here) could accelerate NSC depletion (Pringle 2016) and potentially a risk of carbon starvation even for values of τ well above 0.2.

Overall, asynchrony between (photosynthetic) source and (utilization) sink implies some degree of uncoupling of R, and consequently P_n (and growth), from P and biomass. Carbon demand for metabolism and growth can be mediated by tapping the pool of NSC but only to the extent and to the amount that it is accessible and (surely) usable by plants.

Implications

It has been suggested that the observed decline of P_n during stand development cannot be exclusively caused by increasing respiration costs with tree size (Tang *et al.* 2014). The idea, implicit in the growth and maintenance respiration paradigm – that R_M is a 'tax' that must be paid first and which ultimately controls growth – has also been criticized (Gifford 2003). While this paradigm has some weaknesses (Thornley 2011; Box 2), and is not changed much over the last 50 years despite some theoretical and experimental refinements, no other general and similarly promising mechanistic approach to the modelling of whole-plant respiration has been proposed. Any successful modelling approach for plant respiration must allow plants to steer a middle course between tight coupling to photosynthesis (inconsistent with many observations) and dependence on ever-increasing biomass (risking carbon starvation and death) and the buffering capacity of reserves during carbon imbalances. It seems likely that plants strive to keep an optimal quantity of living

cells that can effectively be sustained by photosynthesis or, when necessary, by drawing on NSC and down regulating allocation to (nonphotosynthetic) metabolically active pools as to minimize maintenance costs (Makarieva *et al.* 2008). This suggests active control on carbon use efficiency and NSC usage by plants and thus on the turnover of the living cells.

Other processes, including hydraulic and nutrient limitations, may be in play (Carey *et al.* 2001; Xu *et al.* 2012). Malhi *et al.* (2015) argued for a link between high whole-plant mortality rates and high forest productivity as ecophysiological strategies that favour rapid growth may also result in fast turnover of trees. However, Spicer & Holbrook (2007) noted that metabolic activity does not decline with cell age and Mencuccini *et al.* (2005) that effects of 'age as such' (including cellular senescence and apoptosis) are probably not responsible for declining *P*, but are linked to the functional and structural consequences of increasing plant size.

To reduce the large uncertainty surrounding this issue, it will be necessary on the one hand to use models that explicitly account for the turnover of biomass and the reserves; and on the other hand, to carry out experimental and field measurements of the dynamics of living cells in wood and reserves availability. These processes have a direct bearing on the stocks and fluxes that drive the carbon balance of forests.

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Tables

Table 1 Underlying modelling assumptions adopted in the analysis

τ level	Corresponding underlying assumption	Reference
$\tau = 0.1$	Low turnover rate, which implies only accumulation of respiring biomass ($i.e. R \propto biomass$)	Reich *et al*. 2006
$\tau = 1$	High turnover rate, with death of cells annually equalling live cell production ($i.e. R \propto P$)	Waring *et al*. 1998
$0.1 < \tau < 1$	Intermediate turnover rate	e.g. White *et al.* 2000, see Box 2
$\tau = 0$	Functionally impossible, because it would imply no mortality of cells	-
$\tau > 1$	Physically impossible, because turnover would exceed the number of available living cells	-

Table 2 Model validation (averages for the years 2006–2010), in brackets standard deviation (when available). Literature data come from Wu *et al*. (2013).

2006-2010 mean (± S.D)	P_n:P	P	R	P_n	P_n*woody*	P_n*litter*	Above Ground-R	Below Ground-R	Above Ground woody stocks	Below Ground woody stocks	Total woody stocks
Units	unitless	g C m^{-2} yr^{-1}							g C m^{-2}		
Literature	0.37	1881 (± 127)	1173 (± 143)	708 (± 65)	307 (± 57)	401	872	301	9885 (± 279)	1848 (± 160)	11733 (± 281)
Modelled	0.45 (± 0.02)	1706 (± 52)	937 (± 30)	768 (± 60)	309 (± 56)	314 (± 9)	635 (± 20)	302 (± 9)	8993 (± 278)	1954 (± 545)	10948 (± 333)

Figures

Fig. 1 Proofs-of-concept for total R_M (a) and live woody biomass accumulation (b) over the course of forest development (time) and increases in size, assuming different live wood turnover (τ, yr^{-1}) rate values, from 1 (W98) to 0.1 yr^{-1} (R06) and including two intermediate values at 0.5 and 0.7 yr^{-1} (e.g. White *et al*. 2000). R_{M_green} (i.e. leaf and fine root R_M) was assumed constant over-time and arbitrarily equal to 2. Summing up R_{M_wood} and R_{M_green} gives the total R_M. Initial woody biomass was arbitrarily considered equal to 10, new annual live wood was also arbitrarily considered equal to 10, $m_R = 0.2$; ($R_M = (W_{live_woody} + W_{green}) \cdot m_R$; see Eq. 3). (b) Initial woody biomass was arbitrarily considered equal to 10, new annual live wood was arbitrarily considered equal to 10. The model is: $W_{live_woody\ (t+1)} = W_{live_woody\ (t)} + \Delta Win_{live_woody\ (t+1)} - \Delta Wout_{dead_woody\ (t+1)}$ (see equation 4 in the main text).

Fig. 2 Model results for (a) P_n:P ratio (dimensionless), (b) net primary production (P_n, g C m^{-2} yr^{-1}) and, (c) autotrophic respiration (R, g C m^{-2} yr^{-1}) performed with varying τ (coloured lines). The beginning of simulations correspond to 1950 (stand age 30 years); the end of simulations correspond to 2100 (stand age 180 years). The dark-pointed red line can be considered as a mechanistic representation of W98's fixed P_n:P ratio (τ = 1 yr^{-1}) while the dark pink line approximates R06's scaling relationship between R and biomass (τ = 0.1 yr^{-1}). Orange dotted lines represent Amthor's (2000) (A00) '*allowable*' range for the P_n:P ratio (0.65 to 0.2). The red dots give the average measured values (Wu *et al.* 2013) at the site for (a) P_n:P ratio, (b) P_n and (c) R. Vertical bars represent the standard deviation with horizontal bars representing the period 2006–2010 (stand age ~ 85–90 years). The shaded area represents the overall uncertainty of model results.

Fig. 3 Regression analyses between whole-plant autotrophic respiration (R, g C m^{-2} yr^{-1}) and (a) whole-plant carbon (W; g C m^{-2}), (b) carbon in living pools ($W_{live_woody} + W_{green}$; g C m^{-2}), (c)

whole-plant nitrogen (W; g N m^{-2}) and (d) nitrogen in living pools ($W_{\text{live_woody}} + W_{\text{green}}$; g N m^{-2}). Different colours represent different τ values as described in the legend panels (with τ = 0.1 yr^{-1}, n = 117; with τ = 0.2 yr^{-1}, n = 149; otherwise n = 150).

BOX 1

The function and dynamics of non-structural carbohydrates

NSC is a surprisingly poorly known component of the whole-tree carbon balance, and commonly disregarded in models (Schiestl-Aalto *et al*. 2019; Merganicova *et al*. *under review*). However, the ability of trees to prioritize storage over growth depends on the role of NSC in allowing temporal asynchrony between carbon demand and carbon supply (Fatichi *et al.* 2014). Such imbalances are assumed to be buffered by drawing down NSC reserves. Recent studies support this assumption, showing that during periods of negative carbon balance (for example during the dormant season, periods of stress, or natural or artificially induced defoliation episodes) NSC is remobilized and transported from the sites of phloem loading, while during periods of positive carbon balance plants preferentially allocate recently assimilated carbon to replenish NSC. Only afterwards is "new" carbon used to sustain growth (Weber *et al.* 2018; Huang *et al.* 2019). Because ultimately plant survival depends more on metabolic carbon demands than on growth, some have argued that all positive carbon flows should be used to replenish NSC at the expense of growth until a minimum NSC pool size (30–60% of the seasonal maximum, Martínez-Vilalta *et al*. 2016) is reached ('active' storage: Sala *et al.* 2012), thus maintaining a safety margin against the risk of carbon starvation (Wiley & Helliker 2012; Huang *et al.* 2019). Note that this assumption departs from the notion that NSC is a mere reservoir for excess supply of carbon relative to growth demand ('passive' storage: Kozłowski 1992). In the model, carbon allocation to all tree structural and non-structural pools is computed here daily and is controlled by functional-constraints due to direct and lagged C-requirements (Huang *et al.* 2019). It is assumed that a minimum NSC threshold level concentration (11% of sapwood dry mass: Genet *et al*. 2010) has to be maintained for multiple functions including osmoregulation, cell turgor, vascular integrity, tree survival (reviewed in Hartmann & Trumbore 2016) and organ-specific phenology (leaf

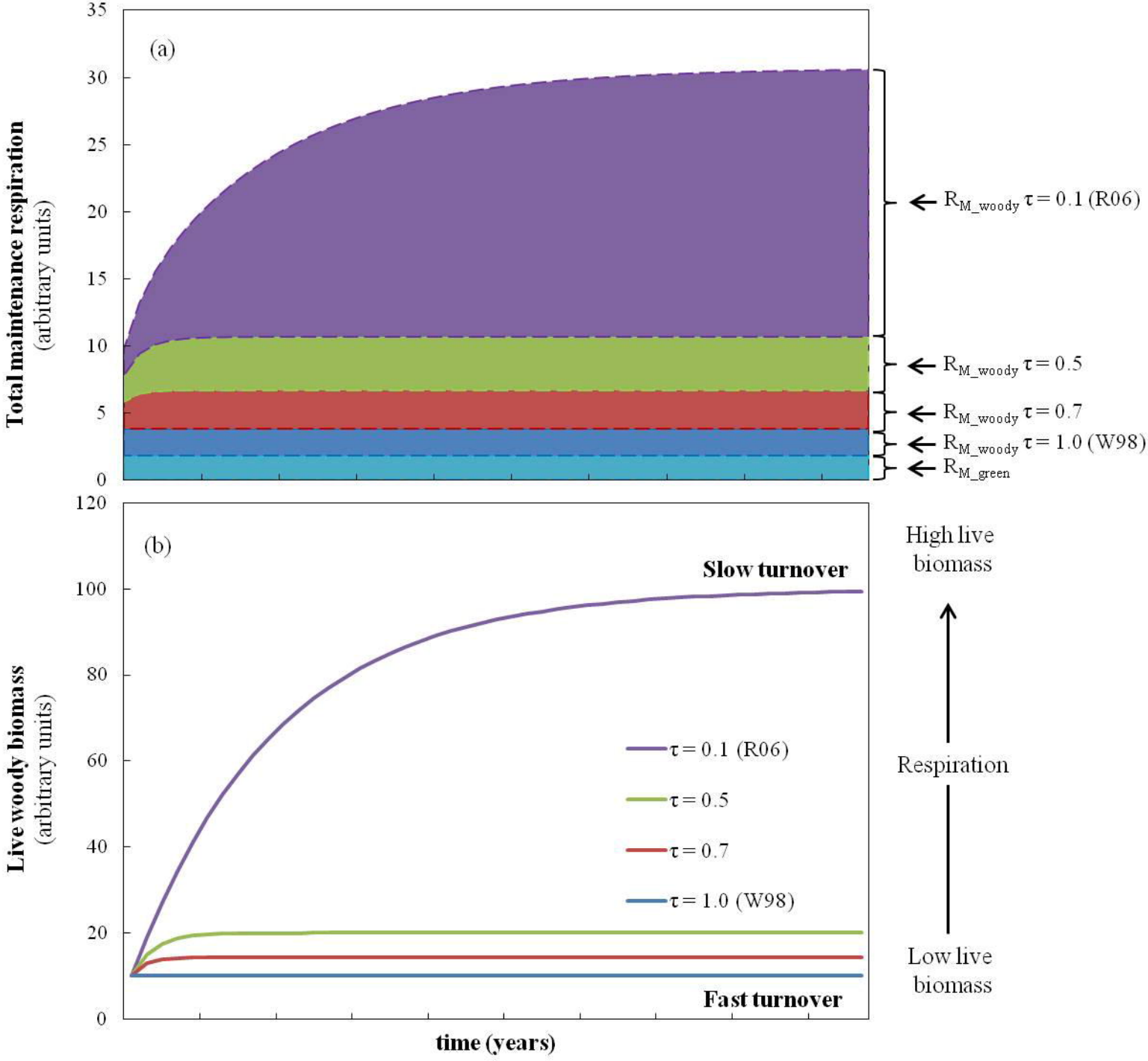
and fine-root formation). The greater the sapwood mass, the greater the minimum NSC threshold must be (Dietze *et al*. 2014). For deciduous trees, four phenological phases are distinguished: (i) the *dormant* phase, where *R* is fuelled by NSC-consumption; (ii) the *leaf onset* phase, when leaf and fine root production consume NSC (unless the carbon balance is positive, in which case new assimilates are used) until the predicted maximum annual LAI is reached; (iii) the *full growing* phase, when new assimilates are allocated to stem, coarse roots, branch, and fruits, and only into the NSC pool if this is below its minimum level; (iv) the *leaf fall* phase, when all assimilates are allocated to the NSC reserve pool while some (~ 10%) NSC is relocated from falling leaves and dying fine roots (Campioli *et al*. 2013). For evergreen species the model follows a simpler schedule consisting of a first maximum growth phase, when the model allocates NSC to foliage and fine roots up to peak LAI, and a second full growing phase, when the model allocates to all of the pools (Kuptz *et al*. 2011). Such patterns of whole-tree seasonal NSC dynamics have been confirmed by Furze *et al*. (2018) and a similar phenological and carbon allocation scheme has been adopted by other models (e.g. Krinner *et al*. 2005; Arora & Boer 2005).

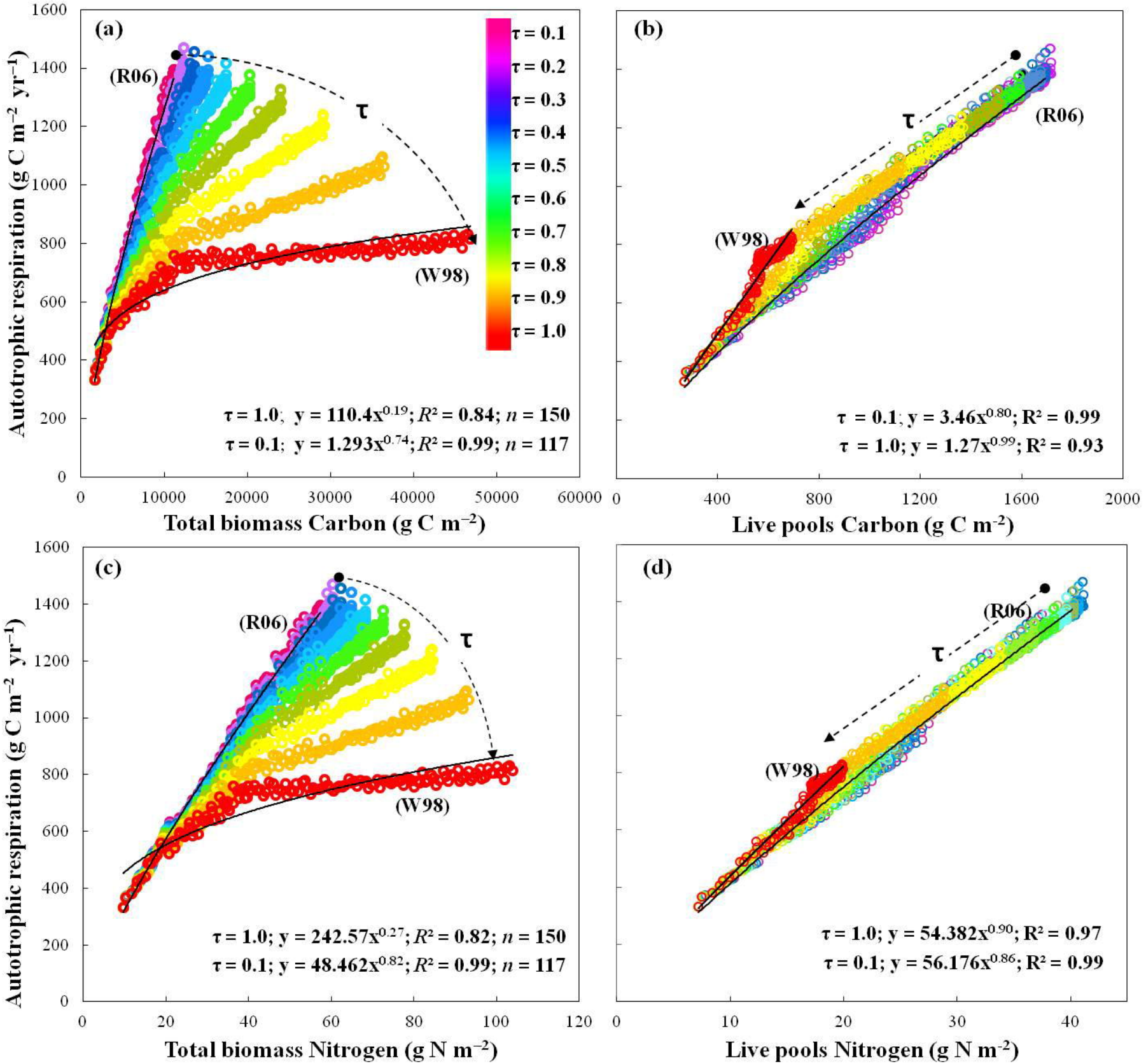
BOX 2

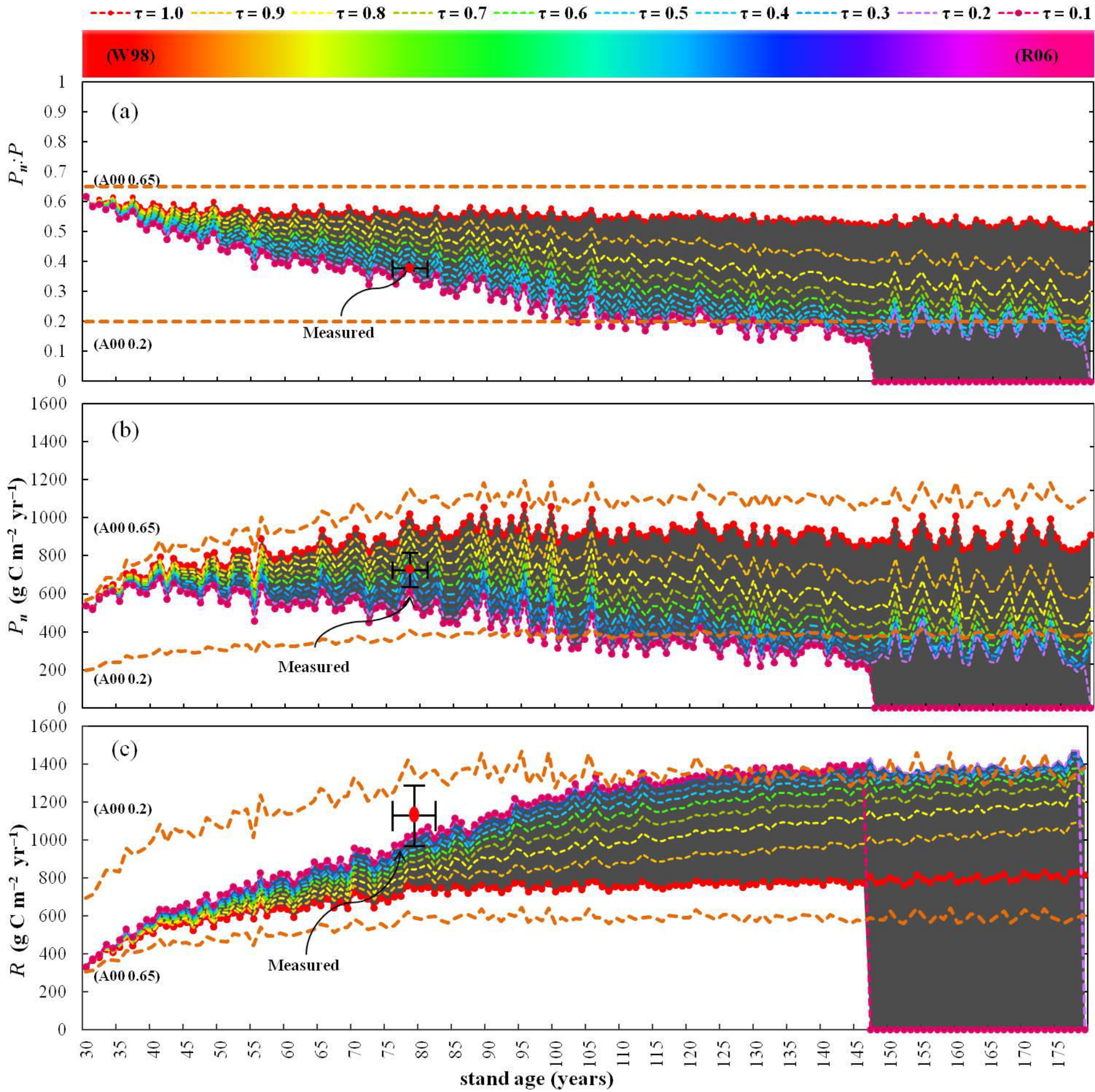
Turnover rates and other uncertainties in models

Most vegetation models assume a fixed rate of sapwood turnover, τ. However, lack of information on this parameter has been shown to be an important source of uncertainty in the modelled carbon balance of vegetation stands (Goulden *et al.* 2011; Malhi 2012; Collalti *et al.* 2019). Values adopted in current models include: τ = 0.7 yr^{-1} in CLM (Oleson *et al.* 2013), Forest v.5.1 (Schwalm & Ek 2004), 3D-CMCC-CNR (Collalti *et al*. 2019) and Biome-BGC (Thornton *et al.* 2002); τ ~ 0.75 yr^{-1} in CASTANEA (Dufrêne *et al.* 2005); τ = 0.85 yr^{-1} in LPJ-GUESS (Smith *et al.* 2001); τ = 0.95 yr^{-1} in SEIB-DGVM (Sato *et al.* 2007), LPJ-DGVM (Sitch *et al.* 2003) and NCAR-LSM (Bonan *et al.* 2003); and τ ~ 1 yr^{-1} in CARAIB (Warnant *et al.* 1994), PnET (Whythers *et al*. 2013), and ORCHIDEE (Krinner *et al*. 2005).

Additional sources of uncertainty include the lack of consideration of a size- or age-related decline in the ratio of living to dead cells (suggesting a declining τ) (Damesin *et al.* 2002; Ceschia *et al.* 2002), the effect of changes in climate (which could temporarily increase τ to reduce maintenance costs in favour of growth: Doughty *et al.* 2015), changes in tissue N and NSC concentrations (Machado & Reich 2006; Thurner *et al*. 2017), and, a probable, genetically controlled down-regulation of basal respiration rates with the ageing of cells (Carey *et al.* 2001; Wiley *et al.* 2017). Moreover, both τ and basal respiration rates (g_R and m_R) are likely to vary among different tree biomass pools (Reich *et al.* 2008). Respiratory carbon losses per unit plant mass may also change to sustain growth as an acclimatory response to carbon demand due to increasing plant size, and perhaps with changing climate (Smith & Stitt 2007). These hypotheses are all grounded in theory, but are supported by very limited observations (Friend *et al.* 2014; Thurner *et al*. 2017).


(a)
Total maintenance respiration
(arbitrary units)
35
30
25
20
15
10
5
0
R_{M_woody} τ = 0.1 (R06)
R_{M_woody} τ = 0.5
R_{M_woody} τ = 0.7
R_{M_woody} τ = 1.0 (W98)
R_{M_green}
(b)
Live woody biomass
(arbitrary units)
120
100
80
60
40
20
0
Slow turnover
Fast turnover
τ = 0.1 (R06)
τ = 0.5
τ = 0.7
τ = 1.0 (W98)
time (years)
High live biomass
Respiration
Low live biomass


(a)
(R06)
(W98)
τ
τ = 0.1
τ = 0.2
τ = 0.3
τ = 0.4
τ = 0.5
τ = 0.6
τ = 0.7
τ = 0.8
τ = 0.9
τ = 1.0
τ = 1.0; y = 110.4x^0.19; R² = 0.84; n = 150
τ = 0.1; y = 1.293x^0.74; R² = 0.99; n = 117
Autotrophic respiration (g C m⁻² yr⁻¹)
Total biomass Carbon (g C m⁻²)
(b)
(R06)
(W98)
τ
τ = 0.1; y = 3.46x^0.80; R² = 0.99
τ = 1.0; y = 1.27x^0.99; R² = 0.93
Live pools Carbon (g C m⁻²)
(c)
(R06)
(W98)
τ
τ = 1.0; y = 242.57x^0.27; R² = 0.82; n = 150
τ = 0.1; y = 48.462x^0.82; R² = 0.99; n = 117
Autotrophic respiration (g C m⁻² yr⁻¹)
Total biomass Nitrogen (g N m⁻²)
(d)
(R06)
(W98)
τ
τ = 1.0; y = 54.382x^0.90; R² = 0.97
τ = 0.1; y = 56.176x^0.86; R² = 0.99
Live pools Nitrogen (g N m⁻²)


τ = 1.0
τ = 0.9
τ = 0.8
τ = 0.7
τ = 0.6
τ = 0.5
τ = 0.4
τ = 0.3
τ = 0.2
τ = 0.1
(W98)
(R06)
(a)
P_n:P
(A00 0.65)
(A00 0.2)
Measured
(b)
P_n (g C m^{-2} yr^{-1})
(A00 0.65)
(A00 0.2)
Measured
(c)
R (g C m^{-2} yr^{-1})
(A00 0.2)
(A00 0.65)
Measured
stand age (years)