

Estimating net biomass production and loss from repeated measurements of trees in forests and woodlands: Formulae, biases and recommendations



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ABSTRACT

There is widespread interest in ensuring that assessment and knowledge of changes in forest biomass, and associated carbon gains or losses, are accurate and unbiased. Repeated measurements of individually-marked trees in permanent plots permit the estimation of rates of biomass production by tree growth and recruitment and of loss from mortality. But there are challenges, for example, *simple* estimates of production rate (i.e., the sum of biomass gain by growth of surviving trees and new recruits divided by census duration) decline as the census interval increases due to unrecorded growth. Even if we allow for these unobserved changes, additional biases may arise due to the non-independence of growth and mortality and to the heterogeneity and compositional changes within the forest. Here we examine these issues and demonstrate how problems can be minimized. We provide and compare alternative approaches to estimate net biomass production and loss from tree growth and mortality. Under the assumption that specific rates of biomass production and loss, i.e., turnover, are constant over time, we derive estimates of absolute biomass turnover rates that are independent of census duration. We show census-interval dependence of *simple* turnover rates grows with increasing specific turnover rates. While the time-dependent bias in *simple* estimates has previously been suggested to increase in proportion to the square of production, we show this relationship is approximately linear. Correlations between stem growth and mortality do not influence our estimates. We account for biomass gain by recruited stems without discounting their initial biomass in production estimates. We can reduce additional biases by accounting for differences in turnover among subpopulations (such as species, sites) and changes in their abundances. We provide worked examples from four forests covering a range of conditions (in Indonesia and Japan) and show the effects of accounting for these biases. For example, over five years in an Indonesian rain forest, *simple* estimates and instantaneous estimates neglecting species heterogeneity underestimated production by 4.9% and 1.6%, respectively when compared to comprehensive (instantaneous species-structured) estimates.

1. Introduction

Forests maintain considerable biomass (Bloom et al., 2016; Houghton, 2005; Pan et al., 2011). This biomass reflects a balance between gains and losses. Quantifying this turnover is key to understanding carbon stocks and dynamics and how they change over time (Bonan, 2008; Phillips and Lewis, 2014). Such understanding is central to scientific evaluations of forest ecosystems and their response to environmental change, as well as to those who view forest conservation, management and establishment as means to reduce atmospheric carbon (Galbraith et al., 2010; McMahon et al., 2010). There are already various schemes where estimated stocks of biomass determine payments to forest owners and others, e.g., “reducing emissions from deforestation

and forest degradation” or “REDD +” (Angelsen et al., 2012). To obtain an accurate picture of how a forest’s biomass and carbon stocks are changing, we require repeated measurements of a representative selection of sites and a suitable way to estimate how gains and losses balance over time. Ideally, in this context, where values determine payments, such estimates of forest biomass stocks and flows would be accurate, reliable, and consistent.

Repeated measurements of individual trees in permanent plots provide records of stem size growth, recruitment and mortality from which forest-level changes can be estimated. Challenges include accurate measurement, consistent standards, context-specific calibration, and accounting for stem dynamics (Chave et al., 2004; Searle and Chen, 2017; Sheil, 1995; Sheil et al., 2017; Sileshi, 2014; Talbot et al., 2014).

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Various reviews have suggested how to improve estimates in practice, for example, standardising recording formats, developing a good understanding of local ecological contexts, and drawing on local knowledge and assistance (Baker et al., 2010; Birdsey et al., 2013; Boissière et al., 2017; Sheil, 1995). Here we focus on the specific challenges resulting from population processes that influence estimates from detailed high-quality plot studies, in which individual stems are monitored over time. Our insights have broad relevance as all changes in biomass stocks reflect the balance of gains and losses.

The production by tree growth (we define our terminology in section 2 below) over a given census period is conventionally estimated as the sum of the above-ground biomass gain of stems that survive (recorded alive in both assessments) and new recruits (recorded only in the second assessment) divided by plot area and census interval (Chave et al., 2003; Chiang et al., 2016; Chisholm et al., 2013; Clark et al., 2001; Kira and Shidei, 1967; McMahon et al., 2010; Poorter et al., 2017; Prado-Junior et al., 2016; Searle and Chen, 2017). In this article, we call this approach the “simple estimate of production by tree growth” (abbreviated to *simple*).

Ideally, rates of biomass production and loss would be characterised using long-term data from large populations of stems that provide sufficient information concerning stand level change. However, as census intervals increase, *simple* estimates of production and loss are increasingly influenced by their neglect of “grow and die” events: that is stems recorded only in the first census, and stems recorded in neither census, which we call “unrecorded production” (Fig. 1). To account for and correct the resulting biases various *ad hoc* procedures have been employed to adjust *simple* estimates according to the length of the census interval (Banin et al., 2014; Chen and Luo, 2015; Johnson et al., 2016; Malhi et al., 2004; Talbot et al., 2014). These studies use data from plots over multiple census periods permitting empirical evaluation of how *simple* estimates vary over census intervals of different duration and employ approaches to extrapolate the value for a theoretical “zero census duration” as their corrected instantaneous rate. These approaches are data intensive, study specific, and thwart simple comparisons. General methods to estimate production and loss rate independently of census interval would be valuable. Our goal here is to devise and illustrate such methods.

Any unbiased estimation approach needs to account for individual-level biomass changes (growth and death) and for population-level processes. Per-capita recruitment and mortality rates need to be defined and estimated independently of the census interval raising concerns regarding the influence of within population variation in growth, mortality and recruitment and compositional change (Kohyama et al., 2018). We know from studies of mortality and recruitment rates that if we ignore any such differences, and assume homogeneity, stand-level estimates become biased (Kohyama et al., 2018; Sheil and May, 1996). Similar biases will arise in estimates of biomass turnover when heterogeneous populations are incorrectly assumed to be homogeneous. Any simple fix may be further complicated by the recognition that individual stem growth and likelihood of mortality are seldom independent: for example, slower-growing trees frequently suffer higher rates of mortality than faster-growing trees (Cailleret et al., 2017; Wyckoff and Clark, 2002); Fig. 1 emphasizes this tendency. Forest stands are generally evaluated only for stems surpassing some minimum size (e.g., in stem diameter or, occasionally, height), which poses the problem of how to estimate recruited biomass in any time interval without knowledge of the stems at smaller sizes (Searle and Chen, 2017; Talbot et al., 2014).

In this article, we propose and examine approaches to estimate stand-level turnover in biomass. For simplicity we focus on above-ground biomass production due to the growth of trees over a minimum diameter. The considerations will also apply to estimates that include other components of biomass such as below-ground stocks. Our approach seeks practical and unbiased estimates and builds on our previous work concerning vital rates: i.e., per-capita recruitment and mortality rates (Kohyama et al., 2018). Here, after we have defined our

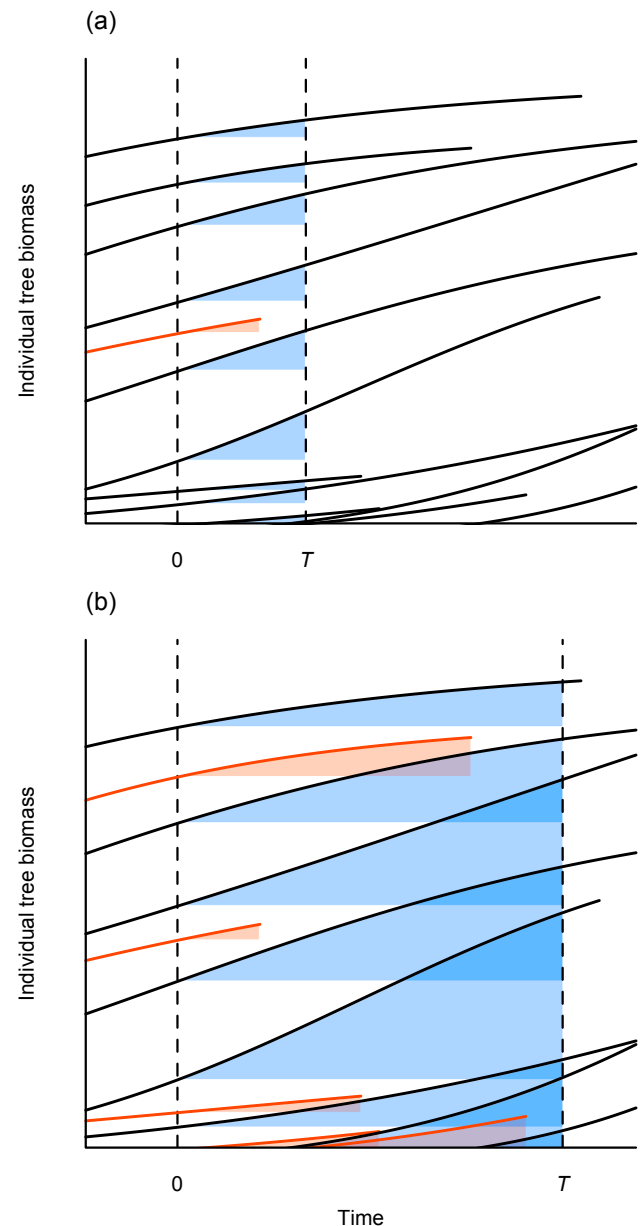


Fig. 1. The effect of census interval on observed stand biomass. (a), Shorter interval; (b), longer interval. Unrecorded growth due to deaths during the period is distinguished from recorded tree growth for survivors and recruits. The *simple* estimate of production by tree growth is the sum of recorded growth only, divided by the time interval. Longer intervals lead to more growth being unrecorded.

terms, we examine how stand-level estimates of biomass production and loss are influenced by growth and survival, by adopted minimum tree sizes, and by stem-level heterogeneity in growth, recruitment and mortality. Our purpose here is to derive and clarify general principles that can be widely applied. We acknowledge that in practice other problems may arise with stems achieving a sufficient size to be included in one assessment and not in the next due to stem shrinkage or breakage that may not imply biological death (Sheil, 2003, 1995). Similarly, a stem considered dead in one assessment might be found to be still alive in a subsequent assessment. We neglect these practical issues here (we recommend they are dealt with and reported in a consistent manner). Our goal is to recommend procedures to estimate biomass turnover and change, which minimise biases and facilitate meaningful comparisons among studies.

Table 1
Biomass turnover rate estimates from repeated censuses of tree biomass.

Turnover rate estimates	Definition ^a	Estimation ^a	Eq.
<i>P</i>	Instantaneous production	$P = pB \text{ w} = \frac{pB_0(e^{rT} - 1)}{rT}$	$\frac{\ln(B_T / B_{S0})(B_T - B_0)}{T \ln(B_T / B_0)}$ (1)
<i>L</i>	Instantaneous loss	$L = lB \text{ w} = \frac{lB_0(e^{rT} - 1)}{rT}$	$\frac{\ln(B_0 / B_{S0})(B_T - B_0)}{T \ln(B_T / B_0)}$ (2)
<i>P</i> _{ann}	Annual production	$P_{\text{ann}} = p_{\text{ann}} B \text{ w}_{\text{ann}} = \frac{B_0(1 - e^{-p})e^{rT} - 1}{T(1 - e^{-r})}$	$\frac{[1 - (B_{S0} / B_T)^{1/T}](B_T - B_0)}{T [1 - (B_0 / B_T)^{1/T}]}$ (3)
<i>L</i> _{ann}	Annual loss	$L_{\text{ann}} = l_{\text{ann}} B \text{ w}_{\text{ann}} = \frac{B_0(1 - e^{-l})e^{rT} - 1}{T(e^r - 1)}$	$\frac{[1 - (B_{S0} / B_0)^{1/T}](B_T - B_0)}{T [(B_T / B_0)^{1/T} - 1]}$ (4)
<i>P</i> _{simple}	Simple production	$P_{\text{simple}} = \frac{B_0 e^{rT} (1 - e^{-pT})}{T}$	$\frac{B_T - B_{S0}}{T}$ (5)
<i>L</i> _{simple}	Simple loss	$L_{\text{simple}} = \frac{B_0(1 - e^{-lT})}{T}$	$\frac{B_0 - B_{S0}}{T}$ (6)

^a *T*, census interval; *B*₀, total biomass at time *t* = 0; *B*_{*T*}, total biomass at *t* = *T*; *B*_{*S0*}, initial biomass at *t* = 0 for survivors over *t* = 0 to *T*; *p*, specific production rate (Eq. (8)); *l*, specific loss rate (Eq. (9)); *r* = *p* - *l*, intrinsic rate of biomass change; *p*_{ann} and *l*_{ann}, specific annual production (Eq. (12)) and loss (Eq. (13)), respectively; period mean biomass *B*_w and *B*_{w_{ann}} are defined by Eqs. (10) and (14), respectively.

2. Terms, definitions and notation

First, we must review and define our terms noting that published usage is sometimes inconsistent and can obscure meaning. The net production rate of standing above-ground biomass (trunk stem, branch and leaf biomass) by size growth and recruitment of new trees has been referred to as “biomass increment” (Clark et al., 2001), “biomass turnover” (Kohyama et al., 2001), or “(coarse) wood production” (Banin et al., 2014; Chiang et al., 2016; Malhi et al., 2004; Talbot et al., 2014). We shall call this “production by tree growth” here. Other studies define “wood production” to be the production of stem and branches only (Jenkins et al., 2001; Miyamoto et al., 2007; Yoneda et al., 1990, 2017). Total net primary production, which we do not address further in this article, is the sum of production by tree growth and the production of fine organs and other organic matter (new foliage, twigs, volatile compounds, etc.) (Clark et al., 2001; Kira and Shidei, 1967). Similarly, we define “biomass loss by tree mortality”, which does not include fine litter fall, loss by herbivory, etc. from living trees. We use “biomass turnover” here to indicate production and loss by stem demography. In any case, the considerations we provide can be adapted for use in other more or less comprehensive frameworks.

In our treatment we assume that we measure the stem diameter of all trees in a defined area (≥ some threshold stem diameter), and indirectly estimate the above-ground biomass of a stem from diameter using biomass equations. Stand-level biomass *B* (Mg ha⁻¹ in dry mass or carbon) is the sum of all living stems in any category divided by plot area. To estimate rates of production and loss (in Mg ha⁻¹ year⁻¹), we require two (or more) censuses separated by an interval of *T* in years. Here, for simplicity, we consider stems as the unit of interest (we consider each stem separately even if trees possess multiple stems). We follow each stem across each census. For each stem over any period defined by two censuses (first and second) three outcomes are possible: survival (recorded in both censuses), death (recorded only in the first census) or recruitment (recorded only in the second census). We require (and shall assume) that the census interval is sufficiently short and that the stems in each subpopulation of interest are sufficiently abundant and long-lived, to ensure that some trees survive over the period.

We denote total biomass *B* at the first and second censuses (at time 0 and *T*) as *B*₀ and *B*_{*T*} respectively. As we have data on all survivors during the census period, and their biomass increment, we have *B*_{*S0*} and *B*_{*S**T*} as the biomass *B* for all survivors at the first and second census, respectively. We also examine the effect of having a non-homogeneous population by considering different subpopulations with distinct properties. We denote these different subpopulation measures with the subpopulation identity *j*, such as *B*_{0*j*}, *B*_{*Tj*}, *B*_{*S0j*}, and *B*_{*S**Tj*}. We use lowercase “*p*” and “*l*” to denote relative rates (year⁻¹) (i.e. specific to biomass) of biomass production by tree growth (including recruitment) and loss by tree mortality, respectively, and capital “*P*” and “*L*” to

denote absolute rates of biomass production and loss (Mg ha⁻¹ year⁻¹), respectively. Subscripts distinguish definitions (e.g., *P*, *P*_{ann}, *P*_{simple}, see Table 1).

3. Estimates of biomass turnover rates and their relationships

Unbiased estimates of demographic processes need to account for the unrecorded “recruit and die” stems that contribute an increasing proportion of stand level changes as census intervals increase (Kohyama et al., 2018; Sheil and May, 1996). Here we apply these considerations (with either continuous or discrete time models) to estimates of demographic biomass dynamics. We shall develop estimation procedures for both “instantaneous” and “annual” rates of biomass turnover, that are, under particular circumstances, independent of census interval. We compare these instantaneous and annual rate estimates with the *simple* estimates that have conventionally been used. Table 1 lists these estimates by Eqs. (1)–(6). We describe each individually.

3.1. Instantaneous estimates

We define instantaneous turnover rates with a continuous-time model of biomass *B* = *B*(*t*) (Mg ha⁻¹) in time *t* (year) such that:

$$dB/dt = (p - l)B = rB, \tag{7}$$

where *p* (year⁻¹) is the specific rate of biomass production, *l* (year⁻¹) is the specific rate of biomass loss, and *r* = *p* - *l* (year⁻¹) is the intrinsic rate of biomass change. Both *p* and *l* are positive by definition, while *r* can be positive, negative or zero. Observed biomass measures correspond to the integration of Eq. (7) from time *t* = 0 to *t* = *T* with *B*₀ as the boundary condition at *t* = 0, which is analogous in form to per-capita instantaneous vital rates for count data (Kohyama et al., 2018; Sheil et al., 1995). Here we obtain

$$p = \ln(B_T/B_{S0})/T, \text{ and} \tag{8}$$

$$l = \ln(B_0/B_{S0})/T. \tag{9}$$

The intrinsic rate of biomass change, *r*, is given by *r* = ln(*B*_{*T*}/*B*₀)/*T*. We define the absolute rates of biomass turnover at any instance *t* by *pB*(*t*) for biomass production and by *lB*(*t*) for loss. For assessing average standing biomass over a period *T*, we estimate the period mean biomass, *B*_w, from *t* = 0 to *T*:

$$B \text{ w} = \frac{B_0}{T} \int_0^T e^{rt} dt = \frac{B_0(e^{rT} - 1)}{rT} = \frac{B_T - B_0}{\ln(B_T/B_0)} \tag{10}$$

Note that (e^{*rT*} - 1)/(*rT*) → 1 when *rT* → 0, and *B*_w = *B*₀ when *rT* = 0. From Eqs. (7)–(9), we obtain the production rate by tree growth *P* = *pB*_w (Mg ha⁻¹ year⁻¹) and of loss by tree mortality *L* to be *lB*_w (Mg ha⁻¹ year⁻¹), thus providing Eqs. (1) and (2) in Table 1.

3.2. Annual estimates

Alternatively, we can define biomass dynamics in a discrete-time “annualised” model using a one-year time step:

$$B_{t+1} = (1 + p_{\text{ann}} - l_{\text{ann}})B_t = \lambda B_t \tag{11}$$

where B_t (Mg ha^{-1}) is biomass at year t , p_{ann} is the proportion of annual production to B_t , l_{ann} is the proportion of annual loss to B_t , and λ is the net annual rate of biomass change. As Eq. (11) corresponds to the one-year integration of Eq. (7), we relate $(p_{\text{ann}}, l_{\text{ann}})$ to (p, l) and we have their estimates from census data as

$$p_{\text{ann}} = e^r(1 - e^{-p}) = (B_T/B_0)^{1/T}[1 - (B_{S_0}/B_T)^{1/T}], \tag{12}$$

$$l_{\text{ann}} = 1 - e^{-l} = 1 - (B_{S_0}/B_0)^{1/T}, \tag{13}$$

and $\lambda = e^r = (B_T/B_0)^{1/T}$ (Kohyama et al., 2018). To estimate the absolute annual production rate, P_{ann} ($\text{Mg ha}^{-1} \text{ year}^{-1}$), and annual loss rate, L_{ann} ($\text{Mg ha}^{-1} \text{ year}^{-1}$), from census data, we obtain annual-mean biomass, $B_{w_{\text{ann}}}$, during the census period from $t = 0$ to $t = T - 1$ (i.e., the sum of every year-initial biomass), by using mathematical induction of geometric series, as

$$B_{w_{\text{ann}}} = \frac{B_0}{T} \sum_{t=0}^{T-1} \lambda^t = \frac{B_0(\lambda^T - 1)}{T(\lambda - 1)} = \frac{B_0(e^{rT} - 1)}{T(e^r - 1)} = \frac{B_T - B_0}{T[(B_T/B_0)^{1/T} - 1]}. \tag{14}$$

Note that when $\lambda = 1$ (thus $r = 0$), $B_{w_{\text{ann}}} = B_0$. By rearranging annual production by tree growth $P_{\text{ann}} = p_{\text{ann}}B_{w_{\text{ann}}}$ and annual loss by tree mortality $L_{\text{ann}} = l_{\text{ann}}B_{w_{\text{ann}}}$, we find Eqs. (3) and (4) in Table 1.

3.3. Simple estimates

The *simple* estimate of biomass production by tree growth, P_{simple} ($\text{Mg ha}^{-1} \text{ year}^{-1}$), assumes time-linear process such that $P_{\text{simple}} = (B_T - B_{S_0})/T$. The corresponding estimate of biomass loss by tree mortality is $L_{\text{simple}} = (B_0 - B_{S_0})/T$. Together with Eqs. (7)–(9), we have Eqs. (5) and (6) in Table 1.

3.4. Relationships among estimates

Here we compare production and loss estimates (see Appendix A further details). If the estimated specific rates of p and l (thus p_{ann} and l_{ann}) are themselves constant over the census period, instantaneous and annual estimates of turnover rates are independent of census interval T . Instantaneous estimates are always larger than annual estimates ($P > P_{\text{ann}}$ and $L > L_{\text{ann}}$), as instantaneous rates include within-first-year production by dying trees while annual rates do not. *Simple* estimates, P_{simple} and L_{simple} , decrease with census interval when p and l are constant, due to the increasing proportion of production that goes unrecorded. *Simple* and instantaneous estimates converge at $T = 0$, while for $T = 1$ *simple* estimates match the annual estimates. Fig. 2a shows their relationships for P 's in idealised forests at equilibrium where $p = l$ (and Fig. A.1 in Appendix A. shows the general cases when $p \neq l$). The T -dependence of *simple* estimates increases with the specific rate of production and loss, p and l (Fig. 2b, Fig. A.1).

The relative bias of *simple* estimates, P_{simple}/P and L_{simple}/L , are decreasing functions of lT and pT , respectively (Eqs (A.3) and (A.4) in Appendix A). When lT and pT are small, the census-interval dependent bias of the *simple* turnover estimates is approximately $P_{\text{simple}}/P \approx 1/(1 + lT/2)$ and $L_{\text{simple}}/L \approx 1/(1 + pT/2)$ (i.e., “the reciprocal approximation”, Eqs. (A.7) and (A.8)), or, $P_{\text{simple}}/P \approx 1 - lT/2$, and $L_{\text{simple}}/L \approx 1 - pT/2$ (i.e., “the linear approximation”, Eqs. (A.9) and (A.10)).

Nonetheless, the rate of net biomass change is the same across the three turnover estimates: $P - L = P_{\text{ann}} - L_{\text{ann}} = P_{\text{simple}} - L_{\text{simple}} = (B_T - B_0)/T$.

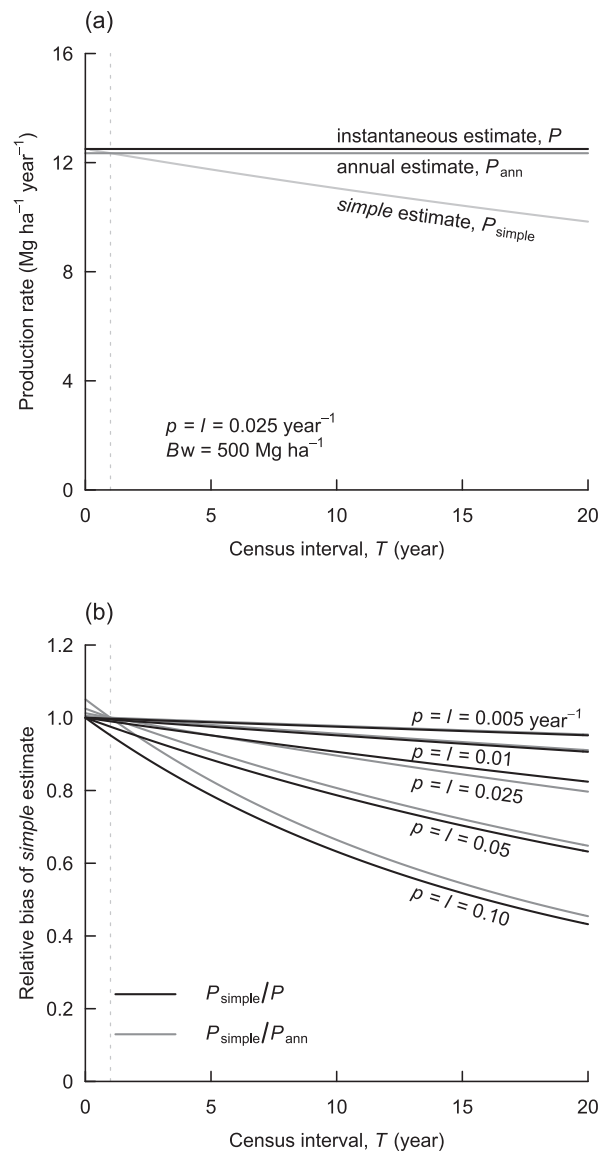


Fig. 2. Three estimates of production rate by tree growth for ideal equilibrium populations, in which specific production rate p is constant and equal to specific loss rate l (thus $r = 0$). (a) Relationship between instantaneous, annual, and *simple* estimates. (b) Census-interval dependent decrease of the *simple* estimate of production, P_{simple} , in which the relative bias of the *simple* estimate over the instantaneous estimate, $P_{\text{simple}}/P = (1 - e^{-pT})/(pT)$, and that over the annual estimate, $P_{\text{simple}}/P_{\text{ann}} = (1 - e^{-pT})/[(1 - e^{-p})T]$. Dashed lines for $T = 1$ year. (Fig. A.1 in Appendix A provides examples when $p \neq l$.)

4. Effects of demographic variation

4.1. Do correlations between growth and mortality influence estimates?

The relative likelihood of a tree dying in a given period is generally not independent of its growth. For example, slower-growing stems often suffer higher mortality than faster-growing stems (Bigler and Bugmann, 2004; Kohyama and Hara, 1989; Rüger et al., 2011; Sheil, 1995; Vanclay, 1994) and tree growth often declines prior to death (Cailleret et al., 2017; Lingensfelder and Newbery, 2009; Wyckoff and Clark, 2002). Thus far, our estimates neglect such links and assume that average growth and vital rates are fixed and independent. We were concerned that this simplification might cause bias.

To assess this concern, we consider an idealized system in which total biomass is divided into two states: active (i.e., fast growth)

biomass B_a and inactive (i.e., zero growth) biomass $B_z = B - B_a$. Active biomass B_a experiences high productivity by growth and recruitment, p_a (> 0) and no loss by tree mortality. In contrast, inactive biomass B_z suffers loss by mortality l_z (> 0) but gains nothing from growth or recruitment. Transition from B_a to B_z occurs at the rate of s (> 0) specific to B_a . The dynamics of biomass can be expressed as:

$$dB_a/dt = (p_a - s)B_a, \quad (15-1)$$

$$dB_z/dt = sB_a - l_z B_z. \quad (15-2)$$

We solve Eq. (15) using linear algebra (see Appendix B). Assuming that $p_a - s > -l_z$ (otherwise, B_a decreases faster than B_z), the biomass ratio of the two states steadily approaches a constant regardless of initial conditions,

$$B_a/B_z \approx s/(p_a + l_z - s), \quad (16)$$

which corresponds to “stable age/stage distribution” in structured population dynamics (Caswell, 2001), and when each of B_a and B_z changes exponentially at the same rate of $r = p_a - s$. Thus Eq. (7) approximates Eq. (15).

We conclude that our instantaneous estimates based on Eq. (7) are uninfluenced by individual-level relationships between productivity and survival, as far as the state ratio B_z/B_a is constant during the census period. When the condition is not met (e.g., the ratio changes due to disturbance), biases remain possible.

4.2. Ingrowth

Census data, and resulting assessments, typically use a minimum size to determine which stems to include. Over a given time interval, some stems which were previously too small, or perhaps had not yet established, gain sufficient size to be included in subsequent assessments—these stems are called “recruits” and their biomass is termed “ingrowth”. The use of a minimum size means that we neglect any biomass that occurs in smaller stems—a more complete evaluation requires a smaller size threshold (Searle and Chen, 2017). In practice there is a trade-off in the effort required to evaluate such stems (local abundance generally increases and biomass per stem declines as size limits are reduced) and all studies require some objective threshold. In this section we shall clarify and address the challenges that arise from the application of any such recruitment threshold.

The specific instantaneous rate of biomass production, p , is the sum of the relative growth rate of resident stems, g (year^{-1}) and ingrowth rate by recruits surpassing the threshold size, b (year^{-1}), relative to standing biomass B , i.e., $p = g + b$. Eq. (7) of our continuous-time biomass turnover expression can then be rewritten as

$$dB/dt = (g + b - l)B, \quad (17)$$

and estimates of g and b are respectively $g = \ln(Bs_T/Bs_0)/T$, and $b = \ln(B_T/Bs_T)/T$ (cf. Eq. (8)). Similarly, we can modify the discrete-time biomass turnover of Eq. (11) to separate growth and recruitment.

This approach to biomass gains by recruitment (Eq. (17)) poses challenges. Ingrowth of biomass during the census period would consist of (i) the biomass of these recruited stems that already exists but is not recorded (as the stems did not yet surpass the size threshold), and (ii) their gain over the census period due to subsequent growth. In a strict sense, only the second is produced during the census interval. Two procedures for estimating the rate of biomass gained due to recruited stems have been suggested. Clark et al. (2001) proposed that the growth of each recruited stem is the difference between its observed biomass at T and the biomass at threshold size. Talbot et al. (2014) examined an alternative approach, in which the growth of a recruited stem over the census is the gain from (unrecorded) initial stem biomass at $t = 0$ to recorded final biomass at T , where the initial biomass is projected from the observed final biomass and the observed growth of other stems around threshold biomass. The estimated production rate using either

of these alternative definitions is always smaller than our P , and production minus loss is always less than the observed net change of biomass (Talbot et al., 2014). Our exploratory analyses thus indicate that these alternative treatments are inconsistent with, and are not readily reconciled with, our search for estimating production rate. Using a simple model similar to Eq. (15), we can show that ingrowth rate is only a portion of the production rate of unrecorded sapling stems (see Appendix C). Therefore, we suggest including ingrowth by recruitment without any additional reduction, i.e., we would advise against the suggested correction proposed by Clark et al. (2001). To avoid any misunderstanding, we underline that our estimates concern only the stand-level biomass above the minimum stem size—those who need to know more about the biomass and behaviours of smaller stems need to record these stems (Searle and Chen, 2017).

4.3. Effects of population heterogeneity

Trees differ in demographic and growth properties depending on species properties and site characteristics. To distinguish such variation in biomass turnover estimation, we employ the same definition of production and loss rate in Table 1 to constituent subpopulation j (this may reflect divisions by species, site, condition or some combination). Total biomass is the sum of subpopulation biomass: $B_0 = \sum_j B_{0j}$, $B_{s_0} = \sum_j B_{s_0j}$ and $B_T = \sum_j B_{Tj}$. When we employ simple estimates (Eqs. (5) and (6)) for each subpopulation j , $\sum_j P_{\text{simple } j} = \sum_j (B_{Tj} - B_{s_0j})/T = P_{\text{simple}}$ and $\sum_j L_{\text{simple } j} = L_{\text{simple}}$ as well, thus simple estimates are not changed with heterogeneity.

In contrast, when we adopt instantaneous (or annual) estimates the values of subpopulations do not simply add to the value given if we ignore subpopulations. Two types of estimation bias, namely “survivorship bias” and “changing-frequency bias”, influence the production and loss rate when we apply Eqs. (1)–(4) ignoring such heterogeneity (Kohyama et al., 2018). Survivorship bias occurs when there is variation in turnover rates among subpopulations in p_j (or $p_{\text{ann } j}$) and l_j (or $l_{\text{ann } j}$). When the size of each constituent subpopulation is constant over time (i.e., values of $r_j = p_j - l_j$ are identical for any subpopulation), survivorship bias causes underestimation of P and L (or P_{ann} and L_{ann}), and the bias grows with census interval (Kohyama et al., 2018; Sheil and May 1996). When the relative abundance of subpopulations changes over time (i.e., r_j -s vary across subpopulations), this raises the additional problem of changing-frequency bias. Varied r_j -s result in increasing abundance for subpopulation with larger r_j , and the instantaneous $r(t)$ for the entire composite population always increases with time t . Changing-frequency bias can oppose, and may even be in approximate balance with, survivorship bias if faster turnover subpopulations (i.e., higher p_j -s and l_j -s) with lower r_j -s are replaced by slower turnover subpopulations but with higher r_j -s (Kohyama et al., 2018). Note that this situation arises in forest succession when a forest progresses from a stand of pioneers, through to a stand dominated by slower growing, more shade-tolerant species (Bazzaz and Pickett, 1980; Finegan, 1996; Nascimento et al., 2005; Rozendaal and Chazdon, 2015). With longer census intervals, the difference between homogeneity estimates (P , L) and the sum of subpopulation estimates ($\sum_j p_j$, $\sum_j l_j$) are expected to increase. For any $T > 0$, $\sum_j p_j > P_{\text{simple}}$ and $\sum_j l_j > L_{\text{simple}}$ (and so for annual vs. simple rates when $T > 1$). Nevertheless, the difference between total biomass production and loss is always equal to the rate of net biomass change, i.e. $\sum_j p_j - \sum_j l_j = \sum_j p_{\text{ann } j} - \sum_j l_{\text{ann } j} = (B_T - B_0)/T$.

We suggest deriving subpopulation-specific instantaneous estimates to reduce these biases. To estimate these rates requires at least one surviving stem for each subpopulation, so it may be necessary to aggregate data from small subpopulations (see Kohyama et al., 2018). For example, in our analyses we aggregate species with fewer than six surviving stems in any census (see next section, and Supporting Information D.1).

Table 2
Period-mean biomass and biomass turnover rates in the four plots in Fig. 3, using *simple* estimation and more sophisticated approaches that account for time and for variation among subpopulations.

Plot	T^*	B_{mean}^*	Bw^*	$\Sigma_j Bw_j^*$	$\langle p \rangle^*$	$\langle l \rangle^*$
Ulu Gadut	19.33	551.3	550.5	545.7	0.0249	0.0180
Tomakomai primary	19.0	156.9	156.9	156.6	0.0143	0.0133
Tomakomai secondary	18.0	108.6	108.2	107.4	0.0224	0.0101
Mt. Onnebetsu	17.0	201.0	201.0	200.9	0.0108	0.00974

* T , the longest interval (year); average biomass measures (Mg ha^{-1}) are $B_{\text{mean}} = (B_0 + B_T)/2$, $Bw = (B_T - B_0)/\ln(B_T/B_0)$ (Eq. (10)), and $\Sigma_j Bw_j$ for structured by species j ; $\langle p \rangle = \Sigma_j P_j / \Sigma_j Bw_j$ (year^{-1}) is period-mean specific production rate; and $\langle l \rangle = \Sigma_j L_j / \Sigma_j Bw_j$ (year^{-1}) is period-mean specific loss rate.

5. Application

We now compare our production and loss rate estimates using real data from four long-term plots (with areas of 0.75–4 ha). We generate *simple* estimates and two-types of instantaneous estimates, i.e., with or without consideration of subpopulations due to species' differences. Our estimates are based on forest-level, above-ground oven-dry mass of main stem, branches and leaves (Table 2, Fig. 3). The data derive from four forests spanning a range of circumstances from equatorial to temperate, and include an old-growth mixed dipterocarp forest in Ulu Gadut, West Sumatra, Indonesia (Yoneda et al., 1990), a primary cool-temperate deciduous forest mixed with spruce in Tomakomai, central Hokkaido, Japan (Uraguchi and Kubo, 2005), a secondary cool-temperate deciduous forest in Tomakomai, Japan (Takahashi et al., 1999), and a subalpine spruce-fir forest on Mt. Onnebetsu in Shiretoko Mountains, eastern Hokkaido, Japan (Nishimura, 2006). We used

allometric equations specific to site/forest-type/life-form to estimate tree biomass from stem diameter (Niiyama et al., 2010; Nishimura, 2006; Takahashi et al., 1999). Appendix D provides further details about the plots, the data collection and the biomass estimation. Supporting Information D.1 provides R code of the turnover-rate calculations with a sample data.

Table 2 compares stand-level period-mean biomass (mean of initial and final biomass B_{mean} , Bw and $\Sigma_j Bw_j$) and specific instantaneous, species-structured production and loss rates for the longest census interval. Theoretically $B_{\text{mean}} > Bw > \Sigma_j Bw_j$, and this was observed though differences were generally small (Table 2).

As we anticipated from our theoretical analyses, *simple* estimates of production and loss rate (P_{simple} , L_{simple}) were smaller than instantaneous estimates, ($\Sigma_j P_j$, $\Sigma_j L_j$) and (P , L) (Fig. 3). The *simple* estimates progressively underestimated turnover with increasing census interval in all data sets. The magnitude of underestimation by *simple* estimates at $T = 5$ years, relative to instantaneous species-structured estimates, i.e. $(1 - P_{\text{simple}}/\Sigma_j P_j, 1 - L_{\text{simple}}/\Sigma_j L_j)$, were (4.9%, 6.7%), (3.1%, 3.3%), (1.9%, 4.2%), and (3.0%, 3.4%) for Fig. 3a, b, c, and d, respectively. The difference among plots reflected differences in specific turnover rates (p , l): these rates were higher in the tropical rain forest compared to the cool-temperate forests (Table 2). The stand-level estimates of instantaneous production and loss rate (P , L) that ignored species-level differences were generally smaller than estimates with subpopulations determined by species ($\Sigma_j P_j$, $\Sigma_j L_j$). Their differences at $T = 5$ years, $(1 - P/\Sigma_j P_j, 1 - L/\Sigma_j L_j)$, were (1.6%, 2.1%), (0.08%, 0.09%), (-0.54%, -1.2%), i.e. over-estimated), and (0.87%, 0.96%) for Fig. 3a, b, c, and d, respectively. The relatively large underestimation by (P , L) in the Ulu Gadut plot indicates the importance of survivorship bias. In contrast in the Tomakomai forests, there was no

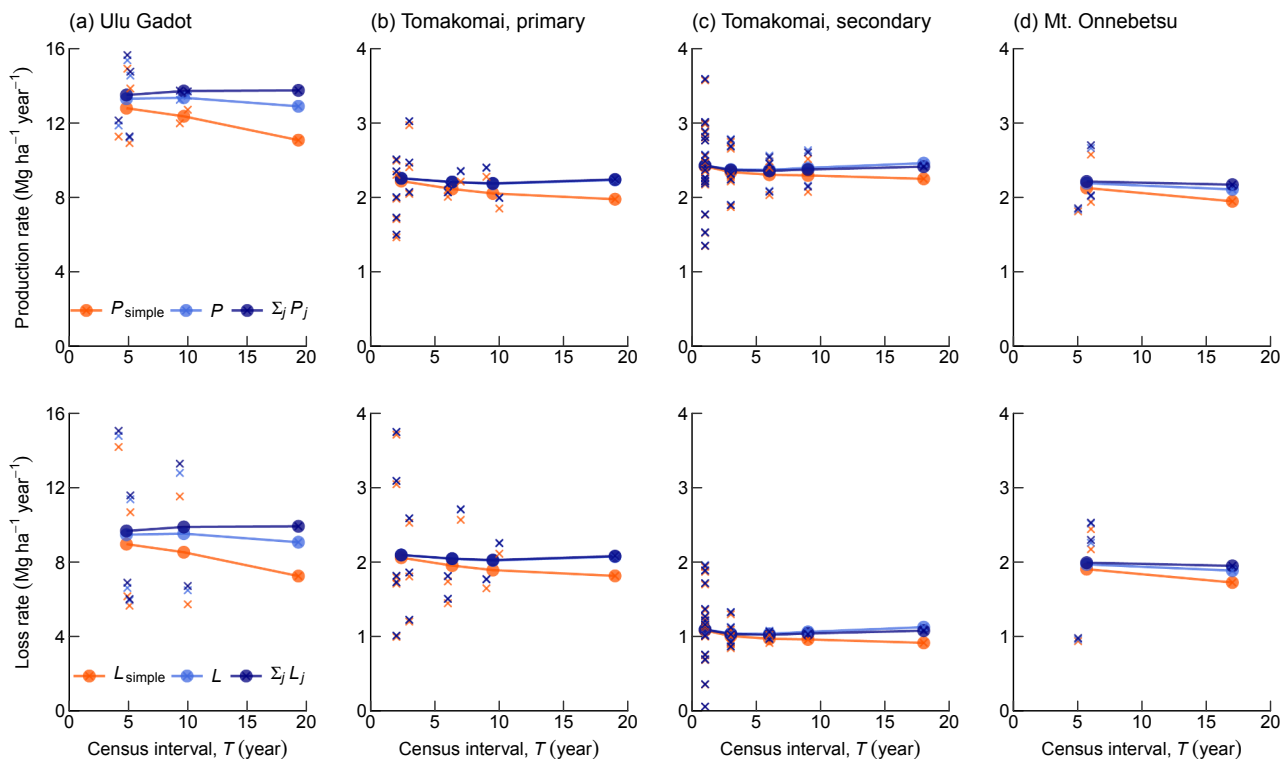


Fig. 3. Estimated rates of production by tree growth and recruitment and loss by tree mortality over census intervals in four forests covering a range of conditions in Indonesia and Japan. (a) Tropical rain forest in Ulu Gadut, West Sumatra, Indonesia (1984–2004, census every ca. 5 years); (b) cool-temperate primary mixed forest in Tomakomai, Hokkaido, Japan (1996–2015, census every 2–3 years); (c) cool-temperate deciduous secondary forest in Tomakomai, Japan (1998–2016, census every year), and (d) subalpine coniferous forest on Mt. Onnebetsu, Hokkaido, Japan (1995–2012, census every 5–6 years). Circles, mean rates over the longest interval (right-hand side circles) subdivided into (quasi-) even subintervals (shorter-interval circles); crosses, subinterval-specific rates. Symbol and line colours indicate differences between *simple* turnover rate (P_{simple} , L_{simple}), instantaneous rates assuming homogeneity (P , L), and the sum of species- j -specific instantaneous rates ($\Sigma_j P_j$, $\Sigma_j L_j$). Note that the range of turnover rates in (a) is fourfold those in (b)–(d) due to higher productivity for tropical rain forest.

clear difference between $(\Sigma_j P_j, \Sigma_j L_j)$ and (P, L) . We speculate that for these plots the effect of survivorship bias was relatively small and/or was largely cancelled out by the effects of the changing frequency among species, particularly in the secondary-stand (Fig. 3c).

6. Discussion

There are many sources of bias in estimating biomass turnover: here we have focused on those that arise from population-level processes when looking at plot-level data with individually-measured stems. We sought robust methods to estimate biomass turnover from plot data that are accurate, reliable, and consistent. Conventional, i.e. *simple*, estimates of biomass production by tree growth and loss by tree mortality, Eqs. (5) and (6), are unsatisfactory as they are not independent of census duration and underestimate change due to unrecorded growth. We have developed and proposed instantaneous (Eqs. (1) and (2)) and annual rate formulae (Eqs. (3) and (4)) that are independent of census interval if we can assume exponential or geometric biomass change (that is constant specific rates of biomass turnover) during the period (Fig. 2). Similar procedures have previously been proposed for quantifying relative gain and loss in stand basal area (Lewis et al., 2004; Marín et al., 2005). We showed that variation in tree growth and survival has little influence on these estimates. We also showed that, in the context of providing logically consistent stand-level estimates of biomass turnover, ingrowth should be incorporated without a threshold-size related biomass correction (in contrast to Clark et al., 2001). We know that our estimates will be biased when the forest is a heterogeneous mixture of subpopulations with distinct biomass turnover characteristics. Our empirical evaluations show that these heterogeneity-related biases in our instantaneous estimates tend to be smaller than the census-interval dependent bias due to *simple* estimates (Fig. 3). Nonetheless, improved estimates can be obtained by combining subpopulation-specific estimates.

Previous studies employed empirical corrections of the *simple* estimate of production rate, P_{simple} , using data from multiple censuses over long periods (Banin et al., 2014; Malhi et al., 2004; Talbot et al., 2014). These studies assumed that P_{simple} decreases linearly with census duration T (cf. our linear approximation), and projected P as the intercept at zero T . Talbot et al. (2014) proposed an empirical correction: $P = (1 + 0.0091 T) P_{\text{simple}}$, which corresponds to our reciprocal approximation, $P_{\text{simple}} = P/(1 + lT/2)$, with $l = 0.018$ (year⁻¹). Malhi et al. (2004) and Banin et al. (2014) suggested that the magnitude of the underestimation of P_{simple} (in basal area) with T , $-d(P_{\text{simple}})/dT$, could be proportional to the square of projected P . In contrast, by our linear approximation, $-d(P_{\text{simple}})/dT \approx lP/2$. We thus expect that the Malhi-Banin prediction, i.e. $-d(P_{\text{simple}})/dT$ is proportional to P^2 , holds when (i) specific loss rate, l , is proportional to specific production rate, p , among plots, and when (ii) projected production rate $P (= pB)$ is not correlated with B across plots. Actually, the data from 50 plots examined by Malhi et al. (2004) (in their Table A2) showed no correlation between P and B (regression probability = 0.22).

Instantaneous and annual rates are distinct. When vital rates are estimated from the same data, annual estimates are smaller than instantaneous estimates (Kohyama et al., 2018; Sheil et al., 1995). For estimating and comparing biomass dynamics, we favour instantaneous rates, because production rate includes within-year ephemeral production (Clark et al., 2001; Kira and Shidei, 1967; Michaletz et al., 2018). However, the difference between instantaneous and annual estimates is small for demographic biomass turnover rates relative to other likely errors in tree measurement and biomass estimation. Old-growth forests typically show specific biomass turnover rates (p and l) of around 0.02 year^{-1} (cf. Table 2), when P_{ann}/P and L_{ann}/L are close to one (ca. 0.99).

To obtain instantaneous (and annual) estimates, we assumed geometric change in biomass over the census period (i.e., constant specific rates of biomass turnover). This assumption follows from simplified

population processes but neglects other influences. In reality, biomass will fluctuate over time due to episodic disturbances, climatic changes, etc. Such fluctuations will lead to inaccuracies that cannot be accounted for in any simple estimation scheme. The assumption of constant rates is also problematic when seasonal patterns occur and census intervals cover non-integral years or when the observation periods and biological cycles do not align and we cannot account for the contribution due to the mismatch (Kohyama et al., 2018). Census intervals should comprise complete years and subsequent analyses should consider the potential influence of seasonal and shorter-term fluctuations in water availability, stem turgor and growth dynamics (Chitra-Tarak et al., 2015; Sheil, 2003, 1997). In the meantime, constant relative change is a pragmatic assumption and reduces biases that arise otherwise (Kohyama et al., 2018).

Despite concern regarding the sequestration capacity and carbon dynamics of forests (Pan et al., 2011), the skills and capacity to generate good quality permanent plot assessments remain localised and near absent in much of the world leading to proposals to use other, sometimes simpler, processes of assessment (Boissière et al., 2017). Our analysis suggests that in this context the added precision provided by detailed permanent plot data regarding the growth and dynamics of individual stems is relatively small (e.g. an underestimate of about 5% of forest production over 5 years – though we acknowledge that this may simply reflect the data we have examined so far. While this result is reassuring, further work will be required to examine when more precise and less-biased estimates are necessary. Indeed, we are confident that biases will increase with variation in the turnover of the constituent species, greater changes in composition and longer census intervals. In any case, detailed species-specific assessments are likely to remain crucial for many aspects of research and for validating simpler approaches. Time-independent methods will, for example, be crucial when we look for trends over time among studies that themselves vary in duration (as has happened with population level dynamics, e.g. Phillips and Sheil, 1997; Sheil and Phillips, 1995).

Is it possible to estimate forest biomass changes accurately, reliably, and consistently? There are many sources of uncertainty in any such evaluations (see, e.g. Chave et al., 2004; Ngomanda et al., 2014; Sileshi 2014; Ishihara et al., 2015; Searle and Chen, 2017; Sheil et al., 2017). The magnitudes of these uncertainties vary with context and cannot be formally evaluated without reference to well calibrated assessments. Such cases are generally lacking and there is still considerable work to be done. We recognise that biases and errors remain a concern and will contribute to uncertainty. Whatever methods are used in any specific case, it is important that all details are recorded to permit meaningful comparisons among studies. Whenever it is practicable, biases should be reduced, and we must seek results that are both reliable and comparable. Our methods can improve estimates of biomass change and turnover and will be especially valuable over longer census intervals and in compositionally heterogeneous and changing stands.

7. Conclusions

We have identified and clarified various biases that arise in the evaluation of biomass dynamics in forest stands and shown how their magnitude may be estimated and reduced. We do not recommend conventional *simple* turnover estimates with or without empirical fixes. We recommend estimates that allow for the time-dependent processes and thus avoid bias: the instantaneous rate of production (Eq. (1)) and loss (Eq. (2)). In situations where time-dependent biases matter, for example in comparing rates from different studies that also vary in duration, we suggest distinguishing between subpopulations (species, sites, etc.) to reduce the uncertain influences caused by demographic heterogeneity and changing composition. These best estimators are

$$\text{Production by tree growth} = \frac{1}{T} \sum_j \frac{\ln(B_{Tj}/Bs_{0j})(B_{Tj} - B_{0j})}{\ln(B_{Tj}/B_{0j})} \quad \text{and} \quad (18)$$

$$\text{Loss by tree mortality} = \frac{1}{T} \sum_j \frac{\ln(B_{0j}/Bs_{0j})(B_{Tj} - B_{0j})}{\ln(B_{Tj}/B_{0j})}. \quad (19)$$

Because any subpopulation j must have at least one surviving stem over the census period, rare subpopulations need to be aggregated until they meet this condition.

Conflicts of interest

The authors declare that there is no conflict of interest.

Appendix A. Relationship among turnover estimates

Here we examine the relationship among our estimates in greater detail. From Eqs. (1)–(6) in Table 1, we explicitly relate our three turnover rates (i.e. *simple*, instantaneous and annual) by means of specific production rate p , specific loss rate l , and census interval T . (Note that the intrinsic rate of biomass change $r = p - l$). Instantaneous and annual turnover rates are related to each other as:

$$P_{\text{ann}}/P = [(1 - e^{-p})/p]/[(1 - e^{-r})/r], \quad (A.1)$$

$$L_{\text{ann}}/L = [(1 - e^{-l})/l]/[(e^r - 1)/r] \quad (A.2)$$

(note that $(e^r - 1)/r = 1$ when $r = 0$). Obviously P_{ann}/P and L_{ann}/L are independent of T , and they are always less than 1 (because $(1 - e^{-y})/y$ is a positive decreasing function for all real y , $(e^y - 1)/y$ is a positive increasing function of y , and because $p > r > -l$).

To compare *simple* turnover rates with instantaneous turnover rates, we have:

$$P_{\text{simple}}/P = [(1 - e^{-pT})/(pT)]/[(1 - e^{-rT})/(rT)], \quad (A.3)$$

$$L_{\text{simple}}/L = [(1 - e^{-lT})/(lT)]/[(e^{rT} - 1)/(rT)]. \quad (A.4)$$

Therefore, $P_{\text{simple}}/P \leq 1$ and $L_{\text{simple}}/L \leq 1$ (equality holds only when $T = 0$) and they decrease with T . Annual and *simple* turnover estimates are related as:

$$P_{\text{simple}}/P_{\text{ann}} = [(1 - e^{-pT})/(1 - e^{-p})]/[(1 - e^{-rT})/(1 - e^{-r})], \quad (A.5)$$

$$L_{\text{simple}}/L_{\text{ann}} = [(1 - e^{-lT})/(1 - e^{-l})]/[(e^{rT} - 1)/(e^r - 1)]. \quad (A.6)$$

The values of these estimates decrease with increasing T , and $P_{\text{simple}} = P_{\text{ann}}$ and $L_{\text{simple}} = L_{\text{ann}}$ at $T = 1$. The time interval-dependent decrease in the value derived the *simple* turnover estimates increases as instantaneous turnover rates (p, l) increase. Fig. 2 illustrates these relationships for the case of equilibrium populations, in which $p = l$.

We can make a first-order approximation by Taylor series expansions for small values of y to show that $(1 - e^{-y})/y \approx y/(e^y - 1) \approx 1 - y/2$ and $(e^y - 1)/y \approx y/(1 - e^{-y}) \approx 1 + y/2$. From this we can approximate the census duration dependent bias of P_{simple} and L_{simple} by reciprocal functions:

$$P_{\text{simple}}/P \approx 1/[(1 + pT/2)(1 - rT/2)] \approx 1/(1 + lT/2), \quad (A.7)$$

$$L_{\text{simple}}/L \approx 1/[(1 + lT/2)(1 + rT/2)] \approx 1/(1 + pT/2). \quad (A.8)$$

And alternatively by linear functions:

$$P_{\text{simple}}/P \approx (1 - pT/2)(1 + rT/2) \approx 1 - lT/2, \quad (A.9)$$

$$L_{\text{simple}}/L \approx (1 - lT/2)(1 - rT/2) \approx 1 - pT/2. \quad (A.10)$$

Fig. A.1 illustrates census duration dependent bias of P_{simple} (Eq. (A.3)) and L_{simple} (Eq. (A.4)), and their reciprocal (Eqs. (A.7) and (A.8)) and linear approximations (Eqs. (A.9) and (A.10)). The reciprocal approximation unlike the linear approximation guarantees a positive value, and approximates P_{simple}/P , better when lT (or pT) is relatively small (Fig. A.1).

Appendix B. Two-stage model assuming active and inactive biomass

Here we analyse Eq. (15) for the two-state biomass dynamics:

$$dB_a/dt = (p_a - s)B_a, \quad (15-1)$$

$$dB_z/dt = sB_a - l_z B_z, \quad (15-2)$$

where B_a and B_z are active and inactive stand biomass, respectively, p_a is specific production rate of B_a , l_z is specific mortality of B_z , and s is the transition rate from B_a to B_z . The coefficient matrix of Eq. (15) has eigenvalues of $p_a - s$ and $-l_z$. We are only interested in the case where $p_a - s > -l_z$ (otherwise, B_a decreases faster than B_z). The solution of Eq. (15) is then

$$B_a = B_{a0} \exp\{(p_a - s)t\}, \quad \text{and} \quad (B.1-1)$$

$$B_z = kB_{a0} \exp\{(p_a - s)t\} + (B_{z0} - kB_{a0}) \exp(-l_z t), \quad (B.1-2)$$

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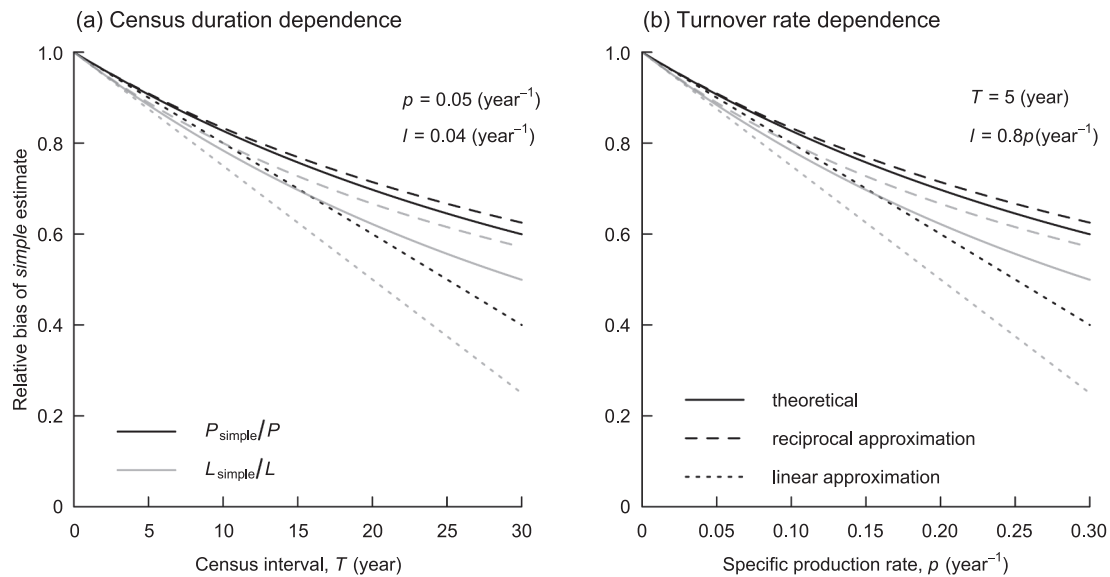


Fig. A.1. (a) Census duration dependence, and (b) turnover rate dependence of *simple* estimates. Full-lines, theoretical functions (Eqs. (A.3) and (A.4)); dashed, reciprocal approximations (Eqs. (A.7) and (A.8)); dotted, linear approximations (Eqs. (A.9) and (A.10)). Two panels are the same besides scale difference of x axis, because these are functions of (pT, lT) .

where B_{a0} and B_{z0} are B_a and B_z at $t = 0$, respectively, and $k = s/(p_a + l_z - s) (> 0)$. From Eqs. (B.1), the biomass ratio of the two states is

$$B_z/B_a = k + (B_{z0}/B_{a0} - k)\exp\{-(p_a + l_z - s)t\}, \tag{B.2}$$

indicating that B_z/B_a approaches k “the stable state ratio” regardless of initial conditions. The ecosystem corresponding to this stable ratio satisfies $B_z \approx kB_{a0} \exp\{(p_a - s)t\}$, and from Eq. (B.1-1) we have

$$B \approx B_0 \exp\{(p_a - s)t\}. \tag{B.3}$$

Therefore, we expect the simple biomass dynamics model of Eq. (7), i.e. $B = B_0 \exp\{(p - l)t\}$, readily approximate the biomass dynamics of Eq. (15), in which demographic variation among trees exists. The mean production p and loss l for overall biomass B (Eq. (7)) are: $p = p_a/(k + 1) = [1 - s/(p_a + l_z)]p_a (< p_a)$ and $l = l_z k/(k + 1) = [s/(p_a + l_z)]l_z (< l_z)$.

Appendix C. Ingrowth model with recorded and unrecorded biomass

To clarify the suitable estimation of production due to ingrowth, we consider a simplified forest that includes two types of biomass: recorded biomass, B , and unrecorded biomass, B_u which consists of sapling stems smaller than the threshold size. Biomass ingrowth by recruitment is the transition from B_u to B . We employ a two-stage model similar to Eq. (15):

$$dB_u/dt = (g_u - l_u - \nu)B_u, \tag{C.1-1}$$

$$dB/dt = \nu B_u + (g - l)B, \tag{C.1-2}$$

where g_u and l_u are production due to sapling growth and loss due to sapling deaths specific to B_u , respectively, ν is the transition rate specific to B_u , and g and l are production by growth and loss by deaths of trees larger than the threshold size, specific to B , respectively. From Eq. (C.1), the absolute rate of biomass ingrowth is $bB = \nu B_u$, where b is ingrowth rate specific to tree biomass B (defined in Eq. (17)).

Eq. (C.1) has two eigenvalues, $g_u - l_u - \nu$ and $g - l$. We assume that $g_u - l_u - \nu > g - l$ (sapling pool as the source of tree stage; note that $g_u - l_u - \nu = g - l + \nu B_u/B$ for any equilibrium forest). From this, the solution of Eq. (C.1) is

$$B_u = B_{u0} \exp\{(g_u - l_u - \nu)t\}, \text{ and} \tag{C.2-1}$$

$$B = \kappa B_{u0} \exp\{(g_u - l_u - \nu)t\} + (B_0 - \kappa B_{u0}) \exp\{(g - l)t\}, \tag{C.2-2}$$

where B_{u0} and B_0 are initial conditions of B_u and B at $t = 0$, respectively, and $\kappa = \nu/(g_u - l_u - g + l - \nu) (> 0)$. The ratio of tree to sapling biomass, B/B_u , is

$$B/B_u = \kappa + (B_0/B_{u0} - \kappa) \exp\{-(g_u - l_u - g + l - \nu)t\}. \tag{C.3}$$

Because $g_u - l_u - g + l - \nu > 0$, Eq. (C.3) implies that in our model forest the ratio B/B_u approaches a constant value κ , regardless of the initial conditions B_0/B_{u0} . More specifically $B \approx \kappa B_{u0} \exp\{(g_u - l_u - \nu)t\}$, where the intrinsic rate of biomass increase is $r = g_u - l_u - \nu = g - l + b$ (cf. Eq. (17)). From Eq. (C.3), we note that the rate of biomass transition, ν , is smaller than biomass production by sapling growth, p_u , which is true as far as $r > -l_u$ (and it is unrealistic to assume that $r < -l_u < 0$). Therefore, the rate of biomass ingrowth by recruits is smaller than the rate of sapling production, i.e. $bB < g_u B_u$.

Our analyses thus indicates that it is reasonable to include b (specific instantaneous ingrowth rate) in Eq. (17) in our estimate of P (instantaneous production by tree growth, Eq. (1)). This is because the instantaneous rate of biomass ingrowth, bB , does not exceed the biomass production by sapling growth, $g_u B_u$, and because biomass gain minus loss, $P - L$, is exactly the net change rate of biomass B for trees above the threshold size. Accordingly, when we quantify the biomass gain and loss of saplings, we need to discount biomass transition to trees, νB_u , in the biomass production

rate of saplings, P_u , i.e., $P_u = g_u B_u - v B_u$ (and the biomass loss rate of saplings is $L_u = l_u B_u$). Total production by tree and sapling growth is thus $P + P_u = pB + p_u B_u$.

Appendix D. Plot census data and biomass estimation

We compared biomass turnover estimates using data from four forests (see Fig. 3). Here we provide further context to these locations, data and estimates. These plots accounted all tree stems over a minimum size. We aggregated species with fewer than six stems for the entire census period (Table 2) to be one “species” in the species-structured turnover rate estimation (cf. Eqs. (18) and (19)).

Fig. 3a shows estimates derived from an old-growth hill mixed dipterocarp forest (“Pinang Pinang Plot”, 1 ha, 590–620 m above sea level, 27.0 °C in mean annual temperature) in Ulu Gadut, West Sumatra (Yoneda et al., 1990). This plot includes 270 species in total (36 with ≥ 6 stems), in which the most abundant species were *Swintonia schwenkii* (emergent species), *Nephelium juglandifolium* (canopy), *Lithocarpus* sp. (canopy), *Shorea maxwelliana* (emergent), *Cleistanthus glandulosus* (understorey), *Mastixia trichotoma* (subcanopy), *Hopea dryobalanoides* (subcanopy), and *Grewia florida* (understorey).

Fig. 3b shows estimates derived from a primary lowland cool-temperate deciduous forest mixed with spruce (4 ha, 80 m a.s.l., 7.1 °C mean temperature) in Tomakomai, central Hokkaido (Uraguchi and Kubo, 2005). This plot has 37 species (25 with ≥ 6 stems), where the abundant species include *Acer mono* (canopy), *Cercidiphyllum japonicum* (canopy), *Acer amoenum* (canopy), *Picea jezoensis* (canopy), *Prunus ssiiori* (subcanopy), and *Fraxinus lanuginosa* (subcanopy).

Fig. 3c shows estimates derived from a secondary cool-temperate deciduous forest (1 ha, 90 m a.s.l., 7.1 °C mean temperature) that grew after clear-felling in 1941 in the Tomakomai Experimental Forest of Hokkaido University (Takahashi et al., 1999). The plot has 31 species (16 with ≥ 6 stems), dominated by *Quercus crispula* (canopy), *Sorbus alnifolia* (subcanopy), *Acer mono* (canopy), *Fraxinus mandshurica* (canopy) and *Prunus sargentii* (canopy early-successional).

Finally, Fig. 3d shows estimates derived from a subalpine spruce-fir forest (total of three 0.25 ha plots, 510–550 m a.s.l., 4.0 °C mean temperature) on Mt. Onnebetsu in Shiretoko Mountains, eastern Hokkaido (Nishimura, 2006). The forest has 10 tree species (6 with ≥ 6 stems), in which the canopy is co-dominated by two conifers, *Picea glehnii* and *Abies sachalinensis*, mixed with *Betula ermanii*, (subcanopy) and *Sorbus commixta* (understorey).

We used data from 1984 to 2004 censuses (every ca. 5 years) for the Ulu Gadut plot, 1996 to 2015 censuses (every 2 or 3 years) for the Tomakomai primary plot, 1998 to 2016 censuses (every year) for the Tomakomai secondary plot, and 1995 to 2012 censuses (5 or 6 years) for Mt.

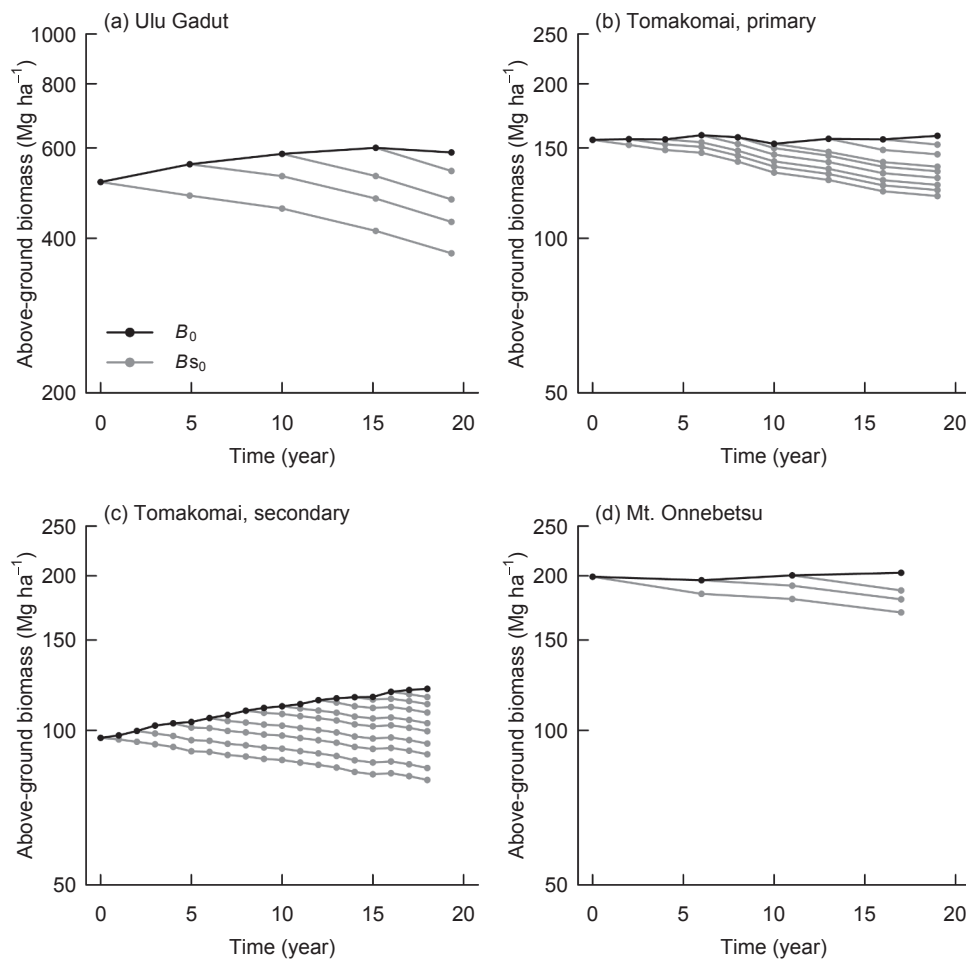


Fig. D.1. Above-ground biomass at each census, B_0 , and its survived fraction recorded in subsequent censuses, B_{s_0} , in four forest plots in Fig. 3. For Tomakomai secondary forest plot, survived biomass B_{s_0} is shown only for censuses of every two years. Note that the range of biomass (log scale) in (a) is fourfold those in (b)–(d) due to higher biomass in tropical rain forest.

Onnebetsu plot. The threshold stem diameter for biomass estimation was 8.0 cm for Ulu Gadut plot and 5.0 cm for other plots. We estimated aboveground biomass from individual stem diameter d (cm). We projected tree top height, h (m), from stem diameter d by extended allometry for each plot,

$$h = 1/[(\alpha d^\beta)^{-1} + \gamma^{-1}], \quad (\text{D.1})$$

where β is allometric coefficient, α (m/cm) is allometric constant, and γ (m) is $h = 1/[(\alpha d^\beta)^{-1} + \gamma^{-1}]$ asymptotic height for infinite stem diameter. We have plot-specific observations of (d, h) for stems that cover the entire range of size variation, and estimated parameters of Eq. (D.1) by non-linear model fitting (function `nls` on R), in which the model with $\beta = 1.0$ was compared to the model with free β in terms of AICc. Estimated α , β , and γ were 2.64, 0.650 and 175 for stems in the Pinang Pinang plot, 1.42, 1.0 and 38.7 for hardwood and 0.82, 1.0 and 52.3 for *Picea jezoensis* stems in the Tomakomai Primary plot, 1.45, 1.0 and 33.0 for stems (all hardwood) in the Tomakomai Secondary plot, and 0.994, 1.0 and 23.0 for hardwood stems and 0.308, 1.26 and 34.1 for *Picea glehnii* and *Abies sachalinensis* in the Mt. Onnebetsu plot. We estimated oven-dry mass of main stem, branches and leaves from d and d^2h for each forest type following guidance from locally conducted studies: Niiyama et al. (2010) for the Ulu Gadut plot, Takahashi et al. (1999) for deciduous trees in the Hokkaido plots, and Nishimura (2006) for conifers in the Hokkaido plots.

Above-ground biomass (B_0) at every census is shown in Fig. D.1, together with the initial biomass for survived stems (B_{S_0}) by subsequent censuses.

Appendix E. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.11.010>.

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