

Recruitment rates in forest plots: Gf estimates using growth rates and size distributions

TAKASHI KOHYAMA and TAKENORI TAKADA*

Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan; and

**Department of International Cultural Relations, Hokkaido Tokai University, Sapporo 005-0825, Japan*

Summary

1 In censuses of tree populations in permanent plots, short census intervals and small population size lead to uncertainty in the observed recruitment rate of a minimum size. Increasing the census interval, however, underestimates the rate because of unrecorded 'recruit and die' events.

2 We propose a new Gf procedure for estimation of recruitment rates. Recruitment rate per area is obtained by multiplication of the density in the smallest size class (f) and the average size growth rate in that class (G) divided by the width of the class. This procedure is valid when the size distribution of the population examined is continuous with size.

3 When tree size structure is negative-exponentially distributed, as is often the case in natural rain forest populations, the Gf estimate of the recruitment rate for a given size class was least biased close to the midpoint size of this class.

4 Gf estimates agreed well with census estimates of recruitment rate from permanent plots in rain forests. A tendency for Gf estimates to be larger than census estimates disappeared when census estimates were corrected for mortality after recruitment.

5 The effects of plot size, census interval and variation in growth rate on estimates of recruitment rate were simulated using model populations. Small plot size caused substantially more among-plot deviation for the census count of recruitment events than for the Gf estimate. The census recruitment rate also showed larger variation among plots for shorter intervals than the Gf estimate, which was independent of census interval. The Gf estimates were therefore more accurate than census counts in many situations. More than several tens of trees were needed in a size class to allow a reliable Gf estimates.

Keywords: demography, model population, rain forests, recruitment rate, size structure, transition rate, tree population.

Journal of Ecology (1998) **86**, 633–639

Introduction

Repeated censuses of permanent forest plots can be used to describe the dynamics of tree populations, i.e. to determine recruitment rate and mortality. There are, however, problems in assessing these rates (Sheil 1995a; Sheil *et al.* 1995; Sheil & May 1996), which raise a debate about whether or not turnover of forests increases with time (Phillips & Gentry 1994; Sheil 1995b; Phillips 1995). These problems arise partly because, in order to obtain demographic estimates in terms of population density, trees from different

environments and of different life-history stages are combined.

One way of avoiding these problems is to incorporate the distribution of tree sizes into demographic analyses, because the fate of individual trees is influenced by both their size and their position in the size structure of the whole forest at a particular census (Kohyama 1992, 1993). Growth rate (usually increase in trunk girth or diameter) can be easily determined from repeated census data for each survivor over the period, providing the position of measurement is marked. However, estimation of mortality in a given size class is less precise because it is obtained on a size-class basis, and will therefore be affected by the sample size. Estimation of recruitment into the mini-

imum size is even more difficult, because the number recruited will vary widely depending on the census timing and plot size.

Precise estimates of recruitment rate and mortality therefore require observation of more trees in large-sized plots, although this carries the disadvantages of increasing the effects of the environmental heterogeneity in space and the large cost of such research efforts. Several such large-scale forest plots with an area of 50 ha or more (Condit 1995; Condit *et al.* 1996) have, however, been established for the purpose of analysing the spatial pattern of populations and estimating demographic parameters using large sample sizes.

Forest studies may use 'stand table analysis' to calculate the transition probability in a given time interval from a particular size class to the next size class; this procedure multiplies the density of trees in a given class by their size growth rate (Vanclay 1994). Similar calculation can be used to estimate recruitment rates from permanent plot censuses. Here we present a theoretical basis for a procedure for estimating recruitment rate into the minimum size class in a small plot. We apply this procedure to census data from actual plots and model plots generated in a computer. We then examine the validity of this procedure by comparing these estimates with census observations of recruitment events.

Estimation of recruitment rates from census data

We obtained apparent recruitment rates simply by counting trees that were smaller than the minimum size at one census but had entered the minimum size at the next census, and by dividing the count by both plot area and time interval between censuses. This census estimate of recruitment rate has two problems. First, if the area of repeated census is small, the number of recruitment events will be limited and suffer huge stochastic variation, particularly in short census intervals. However, the second difficulty arises if the census intervals are long: the census count of recruitment is then inevitably underestimated due to the increase of the fraction that was recruited and then died during the period between censuses (Sheil & May 1996).

The underestimation of census recruitment as a result of mortality can be corrected as follows (Sheil & May 1996). Let us assume that the instantaneous recruitment rate r ($\text{m}^{-2} \text{year}^{-1}$) and mortality after recruitment m (year^{-1}) are both constant with respect to time t . For a census period between 0 and T (year), the ratio of the observed count of recruits at the second census (N_o) to the total number of recruits (N) including those that died before the second census is independent of recruitment rate r and is given by:

$$\frac{N_o}{N} = \frac{\int_0^T r \exp(-mt) dt}{rT} = \frac{1 - \exp(-mT)}{mT}. \quad (1)$$

The ratio is 1 when $T = 0$ and approaches 0 as T approaches infinity. Equation 1 suggests that the census estimates of recruitment rate should be adjusted by multiplying by a factor of $mT/[1 - \exp(-mT)]$, where m is the mortality estimated for the size class around the boundary size. The validity of this procedure of correction is limited by problems in estimation of mortality (Sheil *et al.* 1995; Sheil & May 1996).

Theoretical basis for a new estimate of recruitment rate

Here we show that the recruitment rate at the minimum size of the census can be estimated as the product of the average size growth rate (\bar{G} , cm year^{-1}) of individuals within an arbitrary size class starting from the minimum size and the specific tree density of this class (\bar{f} , $\text{cm}^{-1} \text{m}^{-2}$), provided that size distribution and size-specific average growth rate are continuous functions with respect to size.

If the variance in size growth rate is small, the density of trees, $N(t, x)$ (m^{-2}), reaching size x within the short time interval between $t - \Delta t$ and t , is represented by:

$$N(t, x) = \int_{x - G(t, x)\Delta t}^x f(t, y) dy, \quad (2)$$

where $G(t, x)$ is the average growth rate for size x at time t (cm year^{-1}), $f(t, x)$ is a size frequency distribution ($\text{cm}^{-1} \text{m}^{-2}$), and y denotes any figure of size x for the integral. Figure 1(a) shows this graphically. $R(t, x)$ ($\text{m}^{-2} \text{year}^{-1}$), the rate at which trees grow to reach size x , is $N(t, x)/\Delta t$. $G(t, x)\Delta t$ can be replaced by the size growth Δu and so, when Δt approaches 0, the rate becomes:

$$\begin{aligned} \lim_{\Delta t \rightarrow 0} R(t, x) &= \lim_{\Delta u \rightarrow 0} \frac{G(t, x)}{\Delta u} \int_{x - \Delta u}^x f(t, y) dy \\ &= G(t, x)f(t, x). \end{aligned} \quad (3)$$

Equation 3 shows that the instantaneous recruitment rate is expressed by $G(t, x)f(t, x)$.

Furthermore, the product of the average growth rate (\bar{G}) and the average frequency (\bar{f}) between x and $x + \Delta x$ is represented by:

$$\begin{aligned} \bar{G}\bar{f} &= \frac{\int_x^{x+\Delta x} G(t, y)f(t, y) dy}{\int_x^{x+\Delta x} f(t, y) dy} \frac{\int_x^{x+\Delta x} f(t, y) dy}{\Delta x} \\ &= \frac{1}{\Delta x} \int_x^{x+\Delta x} G(t, y)f(t, y) dy, \end{aligned} \quad (4)$$

where Δx is the width of each size class (Fig. 1b). When Δx approaches 0:

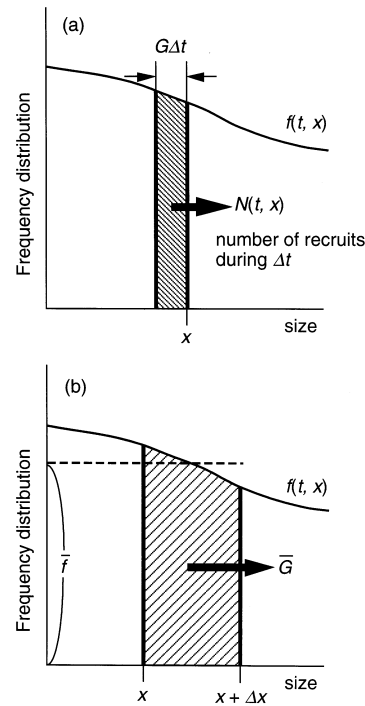


Fig. 1 Gf estimates of transition rate for a continuous size distribution $f(t, x)$ for time t and size x . (a) Transition to size x during time period Δt when all trees grow at rate G ; see equations 2 and 3. (b) Average transition rate, \bar{G} , for the size class between x and $x + \Delta x$; see equations 4 and 5.

$$\lim_{\Delta x \rightarrow 0} \bar{G}f = \lim_{\Delta x \rightarrow 0} \frac{1}{\Delta x} \int_x^{x+\Delta x} G(t, y) f(t, y) dy = G(t, x) f(t, x) \quad (5)$$

Therefore, if x is the minimum size of trees in a sample plot, $\bar{G}f$ should represent the recruitment rate at this minimum size. We call this the growth-frequency estimate (Gf estimate) of recruitment rate.

In practice, the Gf estimate is obtained by multiplying the density of trees in the smallest size class by the average size growth rate for survivors during the census interval, and dividing by the width of size class. The procedure is therefore equivalent to stand table analysis.

Effect of exponential size distribution on recruitment-rate estimation

A Gf estimate can be obtained for any given size class $[x, x + \Delta x]$. However, if $f(t, x)$ is not uniformly distributed with respect to x and Δx is large, the Gf estimate represents the recruitment rate only at a particular size within the class. Here we show that the Gf estimate represents the rate close to the middle of the size class, i.e. at $x + 0.5\Delta x$.

Natural rain forest populations often show the so-called 'reverse-J'-shaped size distribution (Kohyama 1986, 1991), and an exponential decrease in density with size fits well the tree size distribution within a

given range of size. Let us assume that $f(t, x)$ follows an exponential size distribution with respect to x at time t :

$$f(t, x) = K\lambda \exp(-\lambda x), \quad (6)$$

where λ (cm^{-1}) gives the degree (or the slope) of exponential decline of f with x , and K (m^{-2}) is the population density per plot area. The integral of f over the size x is equal to K . We also assume that there is no mortality and that the growth rate G is constant within the class.

Then, the Gf estimate, $\bar{G}f$, for the class $[x, x + \Delta x]$ is:

$$\begin{aligned} \bar{G}f &= G \frac{\int_x^{x+\Delta x} K\lambda \exp(-\lambda y) dy}{\Delta x} \\ &= \frac{KG \exp(-\lambda x)}{\Delta x} \{1 - \exp(-\lambda \Delta x)\}. \end{aligned} \quad (7)$$

We can also obtain the exact recruitment rate at any size z within the size class $[x, x + \Delta x]$ as follows. Applying the same procedure as in equation 2 (Fig. 1a), the expected recruitment rate $R(t, z)$ for the period between t and $t + \Delta t$ at size z is:

$$\begin{aligned} R(t, z) &= \frac{1}{\Delta t} \int_{z-G\Delta t}^z K\lambda \exp(-\lambda y) dy \\ &= \frac{K \exp(-\lambda z)}{\Delta t} \{\exp(G\lambda \Delta t) - 1\}. \end{aligned} \quad (8)$$

The size-width limitation of equation 7 is equivalent to the time-interval limitation of equation 8, which is already shown in general form in the previous section (by equations 3 and 5).

We need to know how large the relative difference of the Gf estimate is from the exact recruitment rate for a particular size-class width Δx . Let us rewrite $z = x + p\Delta x$ ($0 \leq p \leq 1$), so that p is the relative location of the boundary size within the size class for which the Gf estimate is made. For the class $[x, x + \Delta x]$, $b(p)$, the relative difference between the Gf estimate and the exact recruitment rate at $x + p\Delta x$ within that class is represented, from equations 7 and 8, by

$$\begin{aligned} b(p) &= \lim_{\Delta t \rightarrow 0} \frac{\bar{G}f - R(t, x + p\Delta x)}{R(t, x + p\Delta x)} \\ &= \frac{1 - \exp(-\lambda \Delta x)}{\lambda \Delta x \exp(-p\lambda \Delta x)} - 1. \end{aligned} \quad (9)$$

Thus, the relative difference of the Gf estimate is dependent only on $\lambda \Delta x$, and is independent of the size x , growth rate G and population density K .

Figure 2 illustrates the dependence of the relative difference of the Gf estimate at any size within the class on the width of size class Δx and the slope of exponential distribution λ , as predicted by equation 9.

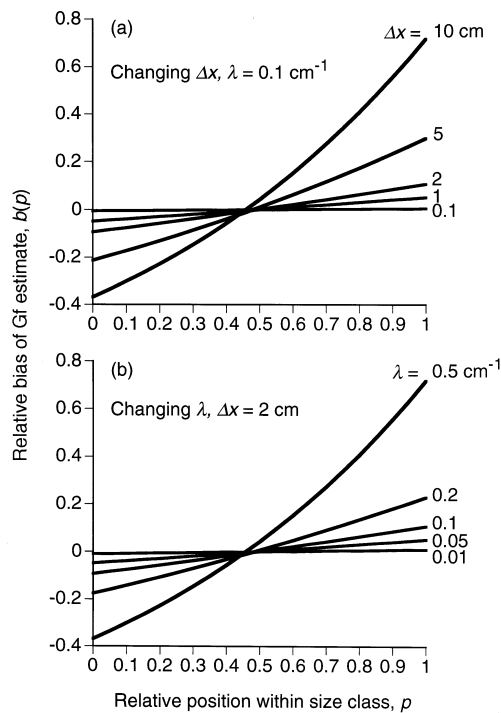


Fig. 2 The relative difference, $b(p)$, between the Gf estimate for the size class between x and $x + \Delta x$ and the recruitment rate expected at any size within the class ($x + p\Delta x$; $0 \leq p \leq 1$), for populations in which size is exponentially distributed within the class (equation 9). (a) Dependence of $b(p)$ on class width Δx (cm); (b) dependence of $b(p)$ on the slope of the exponential size distribution λ (cm^{-1}).

The parameter range examined in Fig. 2 spans values observed in natural rain forest populations. Over such realistic combinations, rates at the mid-point size of the class, $p = 0.5$, were consistently close to the Gf estimate.

Figure 2 also suggests that the deviation of the Gf estimate for a given size class from the actual transition rate is larger at the upper than the lower boundary.

Actual populations

We compared census and Gf estimates for populations of 14 abundant tree species in a warm-temperate rain forest on Yakushima Island, southern Japan (Aiba & Kohyama 1996). Census data from two sites, Segire (0.616 ha; 12-year period 1981–93) and Koyohji (0.450 ha; 10-year period 1983–93), were used: the Gf estimate was calculated for the 2–4 cm class in trunk diameter and the census estimate was obtained from the transition passing through 3 cm in trunk diameter. The results are shown in Fig. 3.

At both sites, a significant correlation was found between census estimates and Gf estimates. The census estimates tended to be smaller than the Gf estimates (Fig. 3a; mean ratio 0.86 ± 0.32 with SD). When census estimates were corrected applying equation 1 with the mortality of the 2–4 cm class of each

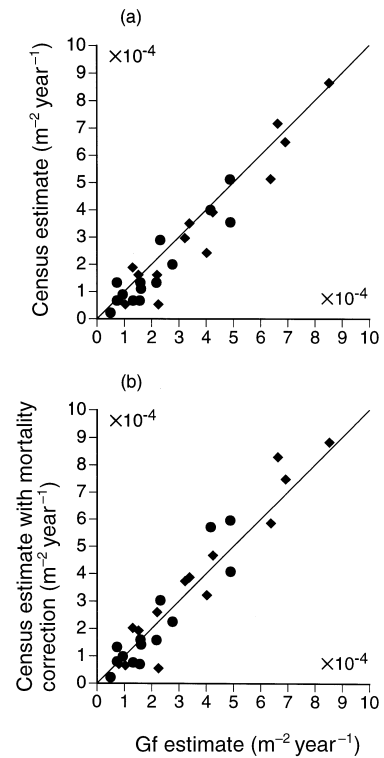


Fig. 3 Relationship between the Gf estimate of recruitment rate from the 2–4 cm class of trunk diameter and the census estimate of recruitment rate across 3 cm in trunk diameter for 14 abundant tree species at two research sites of warm-temperate rain forest on Yakushima Island, southern Japan. Census interval is 12 years for the Segire site (◆) and 10 years for the Koyohji site (●). The diagonal line shows agreement between the two estimates. (a) Census estimate made without correction for mortality; (b) with mortality correction applied as in equation 1 using the mortality for the 2–4 cm size class.

population over the same period (mean \pm SD of $0.028 \pm 0.021 \text{ year}^{-1}$ for the 28 populations), the estimates tended to agree better (Fig. 3b; the ratio now 1.00 ± 0.34).

Agreement between the two estimates was also found for mixed populations of rain forest species, particularly when census estimates were corrected for mortality, as shown in Fig. 4. Data were obtained from two sites in tropical lowland rain forest (cf. Yamada & Suzuki 1996) and two sites in tropical foothill rain forest (cf. Kohyama *et al.* 1989; Kohyama 1991), as well as the warm-temperate rain forest sites shown in Fig. 3.

Simulated effect of growth-rate variation and plot size

To examine the effect of variations in growth rate, plot size and census interval on recruitment rate, sampling plots were computer generated such that tree sizes were uniformly distributed over the range of 0–4 cm trunk diameter. Deterministic growth was modelled by setting the growth rate of trees at $0.05 \text{ cm year}^{-1}$

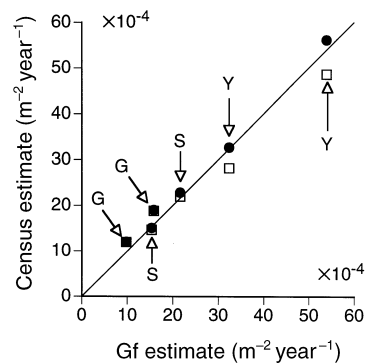


Fig. 4 Relationship between Gf and census estimates of recruitment rate at the class midpoint diameter for all trees irrespective of species in permanent plot censuses. Y, data from two sites in warm-temperate rain forest on Yakushima Island, southern Japan, for the 2–4 cm diameter class (as in Fig. 3) over a 10–12-year period, 1981(83)–93; S, data from two 1-ha plots in tropical lowland rain forest on Gunung Berui, Serimbu, West Kalimantan, for the 5–7 cm diameter class over a 3-year period, 1993–95; G, data from two 1-ha plots in tropical foothill rain forest on Gunung Gadut, Padang, West Sumatra, for the 10–12 cm diameter class over a 3-year period, 1984–87. Census estimates with (●) and without (□) mortality correction according to equation 1.

with no variation. To simulate stochastic growth, the mean growth rate of $0.05 \text{ cm year}^{-1}$ was the same, but this value formed part of a normal distribution with SD of $0.04 \text{ cm year}^{-1}$ irrespective of tree size. These figures are comparable with records from warm-temperate rain forests (Kohyama 1989, 1991). Random numbers generated by a computer were used to give tree size in both models, and growth rates in the case of stochastic growth model.

Plots consisting of either 50 or 200 trees were used to examine the effect of plot size. Zero mortality was assumed for all plots. For both models, we simulated 10-year growth in 20 plots of each size. We obtained census estimates of recruitment events at 2 cm and the Gf estimates for the 2–4 cm class in each plot for census intervals of 1, 2, 5 and 10 years. To examine the effect of plot size on among-plot variation in both estimates, we calculated the coefficient of variation among 20 plots from the expected recruitment rate for an infinite population with uniform distribution.

Figure 5 shows the changes in among-plot variation with census interval. For all time intervals between 1 and 10 years, Gf estimates showed a lower variation than census estimates. For census estimates, variation among plots became larger as the time interval decreased, and was amplified for smaller plots (with a smaller number of trees). By contrast, Gf estimates were independent of time intervals between censuses in simulation (although actual measurement error of growth in Gf estimates can depend on time intervals). The pattern given by the stochastic growth model was quite similar to that of the deterministic growth model. Although the results suggest that in these mortality-free simulations longer time intervals

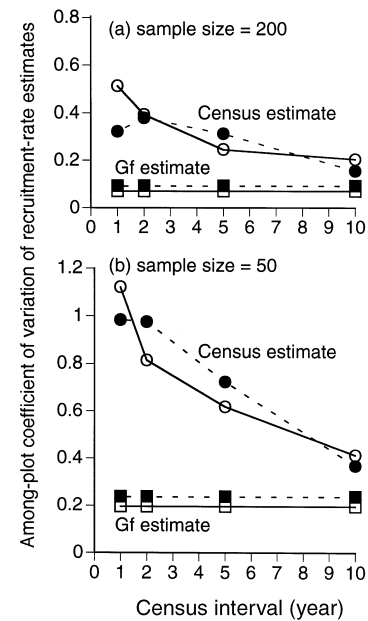


Fig. 5 The coefficient of variation of census recruitment rate and Gf estimate among 20 sampling plots with uniform size distribution over 0–4 cm in tree diameter, as a function of census interval. Closed symbols represent the deterministic growth model, open symbols the stochastic growth model.

give more precise census estimates, recruitment-and-death events mentioned previously (equation 1) would undoubtedly lead to the underestimation census estimates if long periods were applied to real populations.

Simulated effect of within-class population size on the Gf estimate

Although the variation among sampling plots was smaller in the Gf estimate than in census estimate (Fig. 5), the Gf estimate was also affected by the sample size. To evaluate the effect of size class width and to determine the necessary population size within the size class, a further artificial population was simulated: it consisted of 10 000 trees with an exponential distribution whose parameter of decline of frequency with size (λ in equation 6) was 0.230 cm^{-1} . All trees were assumed to grow at $0.05 \text{ cm year}^{-1}$. Gf estimates were obtained for various size class widths using the whole population and subsamples of the population with 1000 and 100 trees.

Size class was set at 2 cm to $2 + \Delta x$ cm, and the density of trees within this class increased almost exponentially with Δx (Fig. 6a). The observed Gf estimate differed markedly from its theoretical value of Gf estimate (from equation 7) when the class width Δx or the population size was small (Fig. 6b). As the number of trees in the class increased, the observed Gf estimate converged to the theoretical value of Gf estimate. A few tens to a hundred trees within the size class (Fig. 6a) were needed to get agreement of observed and theoretical Gf estimates (Fig. 6b).

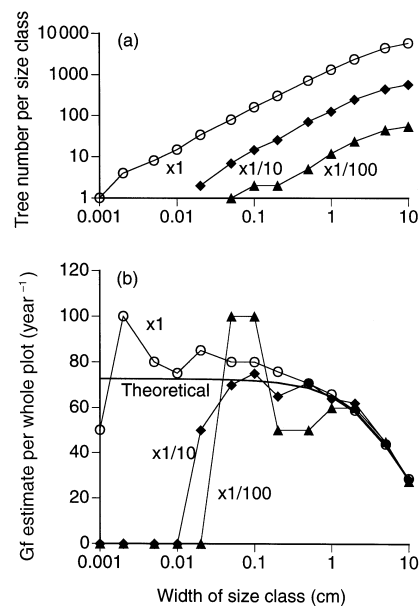


Fig. 6 Dependence of the Gf estimate on the number of trees within a size class; 10 000 trees exponentially distributed with $\lambda = 0.230 \text{ (cm}^{-1}\text{)}$ constitute the whole plot. (a) Number of trees within a size class starting at 2 cm for the whole plot, 1/10 plot (1000 trees) and 1/100 plot (100 trees). (b) Gf estimates for plots with different population sizes and theoretical Gf estimate calculated from equation 7.

Discussion

Simulations of populations of trees in multispecies forests have shown that they are particularly sensitive to species-specific recruitment patterns (Kohyama 1992, 1993). However, the rate of recruitment into a minimum boundary size is not easy to estimate from repeated censuses. Estimation of recruitment is particularly difficult for species-rich rain forests, where many of the species have low abundance and long-term censuses do not necessarily provide better estimates of recruitment rates. When we try to establish a relationship between recruitment rate and environmental conditions such as local crowding, the shortage of data becomes a serious problem. The Gf estimate, however, resolves these difficulties. It is based on one static parameter, tree density in the smallest size class, and one dynamic parameter, average growth rate. Thus, instead of observing a few, often chance, recruitment events, we need only several tens of trees in the minimum size class to determine their frequency and the growth rates of all that survived during a census period, and thus to estimate recruitment rate.

The size frequency dynamics of plant populations have been modelled applying the drift-diffusion equation (Hara 1984; Kohyama & Hara 1989; Takada & Hara 1994):

$$\frac{\partial f}{\partial t} = \frac{1}{2} \frac{\partial^2 (Df)}{\partial x^2} - \frac{\partial (Gf)}{\partial x} - Mf, \quad (10)$$

where t is time, x is size, and $f = f(t, x)$, $D = D(t, x)$, $G = G(t, x)$ and $M = M(t, x)$ are the frequency distribution ($\text{cm}^{-1} \text{ m}^{-2}$), the variance of size growth rate ($\text{cm}^2 \text{ year}^{-1}$), the average size growth rate (cm year^{-1}) and mortality (year^{-1}), respectively. If the variance term is small enough to be neglected, the term second-order differential disappears and equation 10 reduces to the so-called (one-dimensional) continuity equation, which is often applied to forest tree populations (Kohyama 1994). The boundary condition of equation 10 with respect to the minimum size (x_0) is given by:

$$R = \left[-\frac{1}{2} \frac{\partial (Df)}{\partial x} + Gf \right]_{x=x_0}, \quad (11)$$

where $R = R(t, x_0)$ ($\text{m}^{-2} \text{ year}^{-1}$) is the influx rate per unit time per area through size x_0 . Thus estimating $R(t, x_0)$ by the Gf procedure satisfies equation 11 if the differential term of the right-hand side of the equation is negligible. In our simulations, similar results were observed from models with and without growth-rate variation (Fig. 5). This is because the simulations assumed a uniform size distribution for f and size-independent rates for D , thus from equation 11 $\partial (Df)/\partial x = 0$. If, however, the size distribution f follows an exponential distribution, as in equation 6, but D is still independent of size around the boundary of interest, equation 11 can be rewritten as

$$R = \left[\left(\frac{\lambda D}{2} + G \right) f \right]_{x=x_0}.$$

Substituting $\lambda = 0.2 \text{ (cm}^{-1}\text{)}$, $G = 0.05 \text{ (cm year}^{-1}\text{)}$ and $D = 0.0025 \text{ (cm}^2 \text{ year}^{-1}\text{)}$ (typical values for warm-temperate rain forests; Kohyama 1989, 1991), $\lambda D/2$ is very small (0.5%) compared to G , again suggesting that the effect of variation in growth rate around the boundary size is almost negligible compared with the effect of the average growth rate. This explains the agreement between mortality-corrected census estimates and Gf estimates for real populations (Figs 3 and 4). Growth rates for a particular size class of rain forest trees usually have a positively skewed distribution (e.g. Kohyama & Hara 1989), but the observation of real populations (Figs 3 and 4) suggests that this variation is again negligible.

One source of error in the Gf estimate is that the average size growth rate covers only the surviving fraction of trees in the size class examined. Dying trees usually have lower growth rates than those that will survive (Kohyama & Hara 1989), and a long census interval will therefore bring about an overestimation of the recruitment rate. This error in the Gf estimate will be small as long as the census interval is short (but sufficient for precise measurement of growth) so that the ratio of dead trees to all initial trees is small.

Gf estimates are applicable for transition rates across any size. Transition matrices are often con-

structured to analyse the size-structured dynamics of tree populations (Hartshorn 1975; Harcombe 1987; Takada & Hara 1994). When size classes with intervals such as 10-cm d.b.h. are used, the transitions observed between classes will extract only a small portion of data available from repeated censuses, which often make precise measurements (e.g. to 0.1 cm) of diameter growth. Providing these populations have a continuous size distribution, Gf estimates will give a more precise value for transition between size classes.

Acknowledgements

We thank Peter Bellingham, Doug Sheil, Toshihiko Hara, Jerry Halvorsen and David Coomes for their helpful suggestions on earlier manuscripts. This study was supported by grants from the Ministry of Education, Science, Sports and Culture, Japan (nos 07304051 and 09304073 and is a contribution to IGBP-GCTE-TEMA).

References

- Aiba, S. & Kohyama, T. (1996) Tree species stratification in relation to allometry and demography in a warm-temperate rain forest. *Journal of Ecology*, **84**, 207–218.
- Condit, R. (1995) Research in large, long-term tropical forest plots. *Trends in Ecology and Evolution*, **10**, 18–22.
- Condit, R., Hubbell, S.P., Lafrankie, J.V., Sukumar, R., Manokaran, N., Foster, R. & Ashton, P.S. (1996) Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *Journal of Ecology*, **84**, 549–562.
- Hara, T. (1984) A stochastic model and the moment dynamics of the growth and size distribution in plant populations. *Journal of Theoretical Biology*, **109**, 173–190.
- Harcombe, P.A. (1987) Tree life tables. *BioScience*, **37**, 557–568.
- Hartshorn, G.S. (1975) A matrix model of tree population dynamics. *Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research* (eds F. B. Golley & E. Medina), pp. 41–51. Springer-Verlag, New York.
- Kohyama, T. (1986) Tree size structure of stands and each species in warm-temperate rain forests of southern Japan. *Botanical Magazine Tokyo*, **99**, 267–279.
- Kohyama, T. (1989) Simulation of structural development of warm-temperate rain forest stands. *Annals of Botany*, **63**, 625–634.
- Kohyama, T. (1991) Simulating stationary size distribution of trees in rain forests. *Annals of Botany*, **68**, 173–180.
- Kohyama, T. (1992) Size-structured multi-species model of rain forest trees. *Functional Ecology*, **6**, 206–212.
- Kohyama, T. (1993) Size-structured tree populations in gap-dynamic forest – the forest architecture hypothesis for the stable coexistence of species. *Journal of Ecology*, **81**, 131–143.
- Kohyama, T. (1994) Size-structure-based models of forest dynamics to interpret population- and community-level mechanisms. *Journal of Plant Research*, **107**, 107–116.
- Kohyama, T. & Hara, T. (1989) Frequency distribution of tree growth rate in natural forest stands. *Annals of Botany*, **64**, 47–57.
- Kohyama, T., Hotta, M., Ogino, K. & Syahbuddin, & Mukhtar, E. (1989) Structure and dynamics of forest stands in Gunung Gadut, West Sumatra. *Diversity and Plant–Animal Interaction in Equatorial Rain Forests* (ed. M. Hotta), Occasional Paper 16, pp. 33–47. Kagoshima University Research Center for the South Pacific, Kagoshima.
- Phillips, O.L. (1995) Evaluating turnover in tropical forests: response. *Science*, **268**, 894–895.
- Phillips, O.L. & Gentry, A.H. (1994) Increasing turnover through time in tropical forests. *Science*, **263**, 954–958.
- Sheil, D. (1995a) A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. *Forest Ecology and Management*, **77**, 11–34.
- Sheil, D. (1995b) Evaluating turnover in tropical forests. *Science*, **268**, 894.
- Sheil, D. & May, R.M. (1996) Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology*, **84**, 91–100.
- Sheil, D., Burslem, F.R.P.B. & Alder, D. (1995) The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology*, **83**, 331–333.
- Takada, T. & Hara, T. (1994) The relationship between the transition matrix model and the diffusion model. *Journal of Mathematical Biology*, **32**, 789–807.
- Vanclay, J.K. (1994) *Modelling Forest Growth and Yield: Applications to Mixed Tropical Forests*. CAB International, Oxon.
- Yamada, T. & Suzuki, E. (1996) Ontogenic change in leaf-structure and crown form of a tropical tree, *Scaphium macropodum* (Sterculiaceae) in Borneo. *Journal of Plant Research*, **109**, 211–217.

Received 30 July 1997

revision accepted 19 January 1998