

REVIEW

Does biomass growth increase in the largest trees? Flaws, fallacies and alternative analyses

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Summary

1. The long-standing view that biomass growth in trees typically follows a rise-and-fall unimodal pattern has been challenged by studies concluding that biomass growth increases with size even among the largest stems in both closed forests and in open competition-free environments. We highlight challenges and pitfalls that influence such interpretations.
2. The ability to observe and calibrate biomass change in large stems requires adequate data regarding these specific stems.
3. Data checking and control procedures can bias estimates of biomass growth and generate false increases with stem size.
4. It is important to distinguish aggregate and individual-level trends: a failure to do so results in flawed interpretations.
5. Our assessment of biomass growth in 706 tropical forest stems indicates that individual biomass growth patterns often plateau for extended periods, with no significant difference in the number of stems indicating positive and negative trends in all but one of the 14 species. Nonetheless, when comparing aggregate growth during the most recent five years, 13 out of our 14 species indicate that biomass growth increases with size even among the largest sizes. Thus, individual and aggregate patterns of biomass growth with size are distinct.
6. Claims concerning general biomass growth patterns for large trees remain unconvincing. We suggest how future studies can improve our knowledge of growth patterns in and among large trees.

Key-words: above-ground biomass, annual growth rings, artefacts, carbon dynamics, ecological fallacy, monitoring, ontogeny, repeated-measures, statistical methods and inference

Introduction

The growth behaviour of large trees remains poorly known. Improved knowledge offers insights into forest ecology and plant physiology and can advance our understanding of forest productivity, carbon storage and dynamics. Large trees are particularly important in carbon sequestration and timber production (see Clark & Clark 1996; van Rompaey

1997; Lindenmayer, Laurance & Franklin 2012; Slik *et al.* 2013), as determinants of stand level dynamics (Sheil, Jennings & Savill 2000), as habitat (Lindenmayer, Laurance & Franklin 2012; Lutz *et al.* 2012), as sources of fruit and seed and as reservoirs of genetic diversity (Sist *et al.* 2003, 2014). Our limited understanding of tree growth also hinders the interpretation of forest change (Lewis *et al.* 2009; Lapenis *et al.* 2013; Foster, D'Amato & Bradford 2014; Brien *et al.* 2015; van der Sleen *et al.* 2015).

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Until recently, the long-standing wisdom was that the typical lifetime increase in biomass of individual trees was sigmoidal (Assmann 1961; Hyink & Zedaker 1987) with growth following a 'rise-and-fall' unimodal pattern (Vanclay 1994; Weiskittel *et al.* 2011). While such behaviour is established for diameter- and height growth, it is less certain for biomass growth. Increasing biomass growth in young trees – the rising section of the curve – is widely observed. Recent studies have concluded that such increases continue even in the largest stems (see Sillett *et al.* 2010, 2015; Stephenson *et al.* 2014). We set out to examine these conclusions.

We describe challenges to identifying and assessing biomass growth trends in and among the largest individuals of large-stature tree species. The question that motivates us is whether per-stem biomass growth in large individual stems declines or increases. Our intention is to identify and illustrate some of the challenges in assessing patterns in biomass growth of trees, particularly in large tropical trees. First, we briefly review why contrasting trends in per-stem rates of biomass accumulation among the largest trees are of interest. We then highlight and illustrate specific challenges from data collection through to interpretation. As an illustration, we evaluate the lifetime growth trajectories of 706 individual trees for 14 tropical tree species and compare these to aggregate size–growth patterns within each species. In the discussion, we consider our current understanding of tree growth patterns and describe how future studies might be improved.

GROWTH IN LARGE STEMS: BACKGROUND

Decreasing biomass growth in the oldest, largest trees has been widely assumed. Most growth equations used in forest sciences, including those used for individual trees, possess negative terms that reduce growth at large sizes (Assmann 1961; Prodan 1961; Zeide 1993). Such negative terms are necessary for representing the slowing in height and diameter growth that occurs at larger sizes. Empirical justification for their application to biomass growth in individual stems seems less apparent. While observations of declining per-tree volume growth have been documented, see, for example von Guttenberg (1885), and there are observations showing a protracted decline in growth over many years in some larger trees (e.g. Pedersen 1998), systematic accounts are scarce (e.g. Piper & Fajardo 2011). Whether the phenomenon itself is also scarce is unclear.

In contrast, recent studies have concluded that biomass growth increases with tree size. Sillett *et al.* (2010) assessed two of the world's tallest tree species: *Sequoia sempervirens* ($n = 21$) and *Eucalyptus regnans* ($n = 22$). They measured and remeasured each stem at multiple heights after one or more years and concluded that above-ground wood production was greatest in the largest and oldest trees (tree age, but not growth, was inferred from tree rings). A closely related study on *E. regnans* drew comparable conclusions from similar data [$n = 27$ (Sillett *et al.* 2015)].

Stephenson *et al.* (2014) estimated growth from diameter changes on 673 046 stems from 403 tree species mostly recorded in permanent plots. These diameter changes were transformed to estimated biomass growth and were then analysed as an aggregated population for each species against stem size using segmented regression. Biomass growth appeared highest among the largest stems in all but 3% of the species examined. Stephenson *et al.* (2014) also found 'published equations for diameter growth rate in the absence of competition' for 41 temperate tree species and highlighted that 35 of these equations indicate increasing biomass growth with size even at the largest sizes. The authors concluded that biomass growth continuously increases with tree size (Stephenson *et al.* 2014).

Ultimately, trees fail to reach larger sizes because they die or stop growing. Little is known about these processes. Evolutionary ecology identifies various trade-offs among size-dependent costs and benefits (Kohyama 1993; Schwinning & Weiner 1998; Iwasa 2000; Falster & Westoby 2003; Falster, Moles & Westoby 2008). While observations support the idea of such trade-offs (Kohyama *et al.* 2003; Aubry-Kientz *et al.* 2013; Thomas *et al.* 2013; Iida *et al.* 2014; Visser *et al.* 2016), they have failed to identify any fundamental limits to tree size in polycarpic species (Meinzer, Lachenbruch & Dawson 2011). Comparisons among sites and regions suggest the largest sizes that trees can achieve are influenced by many factors. For example, climate and soil can explain around 30% of the variation in humid forest tree height across three continents, with other location-specific factors accounting for another 30% (Yang *et al.* 2016). If fundamental limits are involved, they should manifest themselves in sufficiently large stems through mortality and/or declining growth, though the potentially complex interplay of endogenous and exogenous processes on tree growth and longevity poses challenges (Lee & Muzika 2014).

Limits to tree size and age have been suggested (reviewed in, e.g. Meinzer, Lachenbruch & Dawson 2011; Brutovská *et al.* 2013). Some, such as genetically based senescence, have gained little support. Most discussions focus on physiological and energetic explanations (Ryan & Yoder 1997; Ryan, Phillips & Bond 2006; Peñuelas & Munné-Bosch 2010; Drake *et al.* 2011). Even large well illuminated trees will tend to grow faster if they receive additional light (Graham *et al.* 2003) and most forest trees experience diminishing shade with size (Sheil *et al.* 2006; Prior & Bowman 2014). Thus, tree size, illumination and biomass growth tend to covary in forests. Size-dependent illumination is hard to eliminate, but observations outside closed canopy vegetation may be less affected. Note that a prediction of increasing biomass growth with increasing size may depend on whether shading is, or is not, size-dependent.

So why would growth ultimately decline? Informal perceptions of tree vigour indicate that the crowns on the largest oldest trees are often open and patchy with dieback long before tree death. Formal observations indicate declining foliar efficiency, photosynthetic rates and light

interception (Yoder *et al.* 1994; Niinemets, Sparrow & Cescatti 2005; Nock, Caspersen & Thomas 2008; Drake *et al.* 2011; Quinn & Thomas 2015), and the proportion of intercepted energy invested in stem growth declines with size (Kaufmann & Ryan 1986; Mencuccini *et al.* 2005; Thomas 2010).

Nonetheless, canopy area and total-tree leaf area – and thus implied energy capture – tend to increase as tree size increases (Niklas & Enquist 2002; Xu, Li & Wang 2014). Indeed, total-tree leaf area may increase more rapidly than productivity per unit of leaf area declines – thus allowing increasing growth.

Although metabolic scaling theory (MST) implies increasing energy capture and biomass growth with increasing tree size, it appears of limited use in predicting tree biomass growth in the largest and oldest trees. MST relates a plant's photosynthetic energy capture (P) to stem mass (M), as $P \propto M^{3/4}$, and stem diameter (D), as $D \propto M^{3/8}$, while biomass growth (dM/dt) depends on energy capture, $dM/dt \propto M^{3/4}$ (Enquist *et al.* 1999). Stephenson *et al.* (2014) note that this theory 'predicts that mass growth rate should increase continuously with tree size' and that their log-transformed growth vs. tree mass data appear to fit the predictions of MST. The MST authors recognized their theory as a simplification (see discussion in Price, Enquist & Savage 2007). Single-term power relationships based on stem diameter fail to capture true biomass size relationships (Chambers *et al.* 2001; Chave *et al.* 2005). Such models can capture neither how tree height and tree diameter follow different growth trends (Dawkins 1954; Assmann 1970; Pretzsch 2009) nor how height can decline in very large stems (Hickey, Kostoglou & Sargison 2000). When applied to stand dynamics, MST failed to predict stem size distributions at the largest stem sizes 'likely because of non-competitive sources of mortality not included in the model' (see legend to fig. 3, p. 7049 in Enquist, West & Brown 2009). Similarly, MST-derived predictions for size–growth trends for individual open-grown trees at near-maximum sizes are lacking. Thus, beyond its own insufficiency, MST offers no insights into tree biomass growth trends at near-maximum sizes.

To conclude, there is considerable theoretical and empirical uncertainty regarding how biomass growth might vary with stem size. Furthermore, given the diversity of tree species, evolutionary histories and environments, a common growth pattern is not necessarily expected. Further research will be required to clarify these issues. Here, drawing on past studies, we examine some underappreciated challenges and pitfalls of determining biomass growth trends in large trees.

SCARCE STEMS AND EPHEMERAL PROCESSES

Determining the biomass growth trends of large trees requires sufficient measurements of such trees. Larger stems of most tree species become increasingly scarce with size (de Liocourt 1898; Clark & Kellner 2012). In old-

growth forests, stem densities typically halve with every 10-cm increase in the diameter size limit (Enquist & Niklas 2001; Niklas, Midgley & Rand 2003), implying that we should not expect one stem larger than half the maximum size (exceeding 1 m diameter) even if we locate 100 stems >10 cm diameter. Thus, the largest stems are poorly represented unless special measures are used to locate them (Roesch & Van Deusen 2010). Untargeted low percentage coverage with plots is likely to be inadequate for detecting the largest stems for most species.

We may also have difficulty detecting large stems in growth decline because such situations are short-lived. Many studies show that mortality rates rise when growth rates decline (e.g. Vanclay 1994; Wyckoff & Clark 2002; Bigler & Bugmann 2004; Rüger *et al.* 2011). This is expected as reduced growth implies reduced vigour, and whether associated with senescence or not, reduced vigour implies increased vulnerability to threats such as pests and pathogens (Guérard, Dreyer & Lieutier 2000; Hooper & Sivasithamparam 2005; Knapp, Soule & Maxwell 2013). Additionally, there is a semantic concern. Unless death is an instantaneous consequence of an external cause (e.g. wind), it seems implausible that stems might increase in growth until death. An ephemeral 'decline before death' behaviour may be judged a 'trivial' detail and not a 'true' trend, but the decline may be protracted (e.g. Pedersen 1998; Dobbertin 2005) – and the generality of these processes and their time scales remain unclear. In any case, a failure to observe growth declines in a small sample of large trees is insufficient to distinguish if they are brief and or rare, or absent.

CALIBRATIONS: CONVENIENCE VS. CONFIDENCE

Relationships between measured diameter changes and estimated biomass growth rely on accurate calibration (Sileshi 2014). Variation in architecture and form, ontogeny, bark thickness, wood density, damage and rot all contribute to variation within and among species. Whereas generalized diameter–biomass relationships are convenient for estimating the biomass of mixed stands, they are inappropriate for inferring subtle behaviours within individual species and populations (Clark & Kellner 2012; Magnabosco Marra *et al.* 2015). Species-specific calibration errors may cancel each other out to some extent when general biomass relationships are used in mixed stands, but the errors can still be substantial (e.g. Ngomanda *et al.* 2014). Such calibration errors can readily dominate implied biomass growth for individual stems and populations.

Similar stems may have very different biomass–diameter relationships. Wood density can vary substantially in both radial and vertical dimensions (Wassenberg *et al.* 2015), and hollows can be considerable. Density, and hence implied biomass growth by size, varies within stems of most species (Wiemann & Williamson 1989; Nock *et al.* 2009; Williamson & Wiemann 2011; Hietz, Valencia & Joseph Wright 2013; Schüller, Martínez-Ramos & Hietz

2013; Plourde, Boukili & Chazdon 2015). The wood density of *Liriodendron tulipifera* L. increases fourfold as the stem grows (Wiemann & Williamson 1989). Other species show decreasing stem wood density with size (Nock *et al.* 2009), and some are naturally hollow, for example *Cecropiaceae* and *Caricaceae*. These contrasting species-specific patterns cannot be captured in generalized diameter–biomass relationships and can bias biomass growth assessments. For example, imagine taking a biomass–diameter function that fits *Liriodendron tulipifera* and applying it to species with decreasing wood density with size. The resulting estimates would see biomass growth as ‘increasing’ even when it is constant. Similarly, a function that fits a species with decreasing density with size would imply ‘decreasing’ biomass growth in *Liriodendron tulipifera* even when it is constant.

Equations for linking biomass to stem dimensions should not be used outside their range of validity as determined by calibration (Ishihara *et al.* 2015). This is a special challenge for very large trees as few, if any, such stems tend to be used in calibration, and increasing size is associated with increasing variation in stem biomass. This increased variation reflects buttressing and stem form (Sheil 1995), the proportion of biomass in tree crowns (Ploton *et al.* 2015) and the prevalence of stem damage, rot and hollows (Remm & Löhmus 2011). These factors vary not just by size but by species and location (see, e.g. Heineman *et al.* 2015). A majority of larger stems can be substantially affected by rot in some locations (Whitford 2002). Hollows, rot and damage tend to increase in individual stems and can thus reduce net biomass gains; production of new wood will be impacted when growing tissues are lost and damaged (Chambers *et al.* 2001), and/or considerable energy is required to sustain good health. Few large trees are included in calibrations and those that are may not be representative of the population as a whole (e.g. regarding the inclusion of broken or unhealthy trees (Clark & Kellner 2012; Goodman, Phillips & Baker 2013). For instance, Chave *et al.* (2005)’s widely used biomass–diameter equations were compiled from various studies but included only 14 trees of more than 100 cm d.b.h. and none larger than 200 cm. Indeed, the authors noted that their models are only **valid in the range 5–156 cm for D** and indicated that their equations appear to overestimate biomass among the largest stems (Chave *et al.* 2005). Any study extrapolating these equations to larger sizes is unreliable.

Generalized size–biomass equations are approximations and will always include some errors that may be influential. Consider the moist forest (volume) equation of Chave *et al.* (2005): if the parameters are adjusted by just 1% (the positive terms increased and the negative terms reduced), then the rate of volume change with diameter change on a 2-m-diameter stem increases from 48 to 54 cm³ mm⁻¹ while the first and second differentials with regard to diameter (that will influence the rate of change and thus any growth maximum) shift from 0.013 to

0.015 cm³ mm⁻² and from –10.7 to –12.1 cm³ mm⁻³, respectively. Hence, we see that small errors (only 1% in this case) in the constants defining size–biomass relationships can change growth and growth per unit size by 10–20% in large stems. Such distortions could dwarf genuine trends. The influence of such biases is case-specific and cannot be known without extensive calibrations for specific populations. Furthermore, when the same estimation function is used for discerning growth patterns in multiple species or populations, the resulting estimates lack independence due to the errors resulting from that function. In any case, assessments of biomass growth trends in large stems of one species at one site cannot be robustly inferred from the study of smaller stems of other species in other sites.

ERROR, QUALITY CONTROL AND BIAS

The evaluation and analysis of tree growth have recognized complexities (Furnival 1961; Hurd 1979; Vanclay 1994; Sheil 1995; Kangas 1996; Williams 1997; Herault *et al.* 2011; Bowman *et al.* 2013). For example, although logarithmic-transformation is often useful in analysing tree growth (e.g. Brien, Zuidema & Martínez-Ramos 2010), it must be used with caution as it requires removal of negative biomass growth observations and results in confidence intervals lacking natural units for the quantity of interest (see also, Packard, Birchard & Boardman 2011). Here, we shall focus on data correction and quality control.

The diameter changes assessed in tree growth studies are typically small and readily distorted by errors (Sheil 1995, 2003; Eastaugh & Hasenauer 2013). Precise measurements, even when conducted carefully in quick succession, are seldom exactly equal. While impressive consistency is possible (e.g. Clark, Clark & Oberbauer 2010) and various ways to account for errors have been developed (e.g. Rüger & Condit 2012), discrepancies cannot be eliminated. The resulting ‘noise’ depends on both the stem (damage, bark shedding, water status) and the measurements (the path of the tape, limits to precision and rounding) (Sheil 1995). Such measurement noise generally increases with stem size (Sheil 1995, 1997, 2003), with the largest stems being the most challenging (Fig. 1). Large stems are sometimes excluded from analyses due to such problems (e.g. Condit, Hubbell & Foster 1993). When assessing growth in the largest stems, we must use these data while recognizing their inaccuracies. Consider measuring Sillett *et al.* (2010)’s largest stem (stem 27) at 20 m above the ground: the tape should follow the same track around the >6-m circumference. A different millimetre rounding decision results in a 158 kg biomass difference: about 20% of this tree’s reported 784 kg annual growth. Larger changes may reflect stem moisture status (Sheil 2003; Pastur *et al.* 2007). Longer measurement intervals can reduce the influence of such errors; thus, we note that in fig. 5 of Sillett *et al.* (2010), the two *E. regnans* trees (25 & 26) with lowest growth were



Fig. 1. Precision measurement of large tree stems is frequently challenging with buttressed, winged and flared stems, ladder access, hollows, loose bark, insect nests, lianas and epiphytic vegetation. Images are clockwise 1. Australia (Doland Nichols), 2. Indonesia (Nurul Winarni), 3. Uganda (Badru Mugerwa), 4. Peru (Benjamin Drummond), 5. Sarawak (Lan Qie) and 6. Costa Rica (David Clark).

also the only two measured over a longer multiyear period and are thus evaluated with the least uncertainty. The use of only one measurement interval to indicate growth also provides no way to distinguish general trends from the impacts of climatic and other events – something that should be possible with longer measurement series (see, e.g. Clark & Clark 2011).

As inaccurate stem measurements can distort fitted relationships, so various approaches are used to find and correct such measurements. Often measurements are compared with previous observations while still in the field so that any discrepancies are addressed promptly and cheaply (Vanclay 1991). Implied measurement changes are typically checked again during computer filing so that less-plausible values can be identified. Further checks can occur before analysis to exclude, adjust or correct unlikely values. While some of these processes may be well defined and documented, some rely on informal judgement. Such data controls are a double-edged sword: removing anomalies but adding bias. A

moderate positive error on a slow growing stem will not trigger concern, whereas a negative error of similar size on the same stem indicates shrinkage and is flagged for revision. While reasonable – negative growth is seldom a true reflection of biomass changes – this asymmetrical correction distorts size-related patterns. Consider an error (ϵ) in the measurement of a true diameter change (ΔD). For basal area (BA), the discrepancy increases with stem diameter (D): that is $BA \propto D(\Delta D + \epsilon)$, where $D\Delta D$ is proportional to true change and $D\epsilon$ is the additional term due to error. As a stem size increases, both D and the mean magnitude of ϵ increase, leading to an increasing multiplicative error $D\epsilon$. As ϵ is more often positive than negative, an increasing volume growth vs. size relationship results (Fig. 2).

INDIVIDUALS AND AGGREGATES

Depending on context, both aggregate and individual values may be of interest, but they must not be confused. The

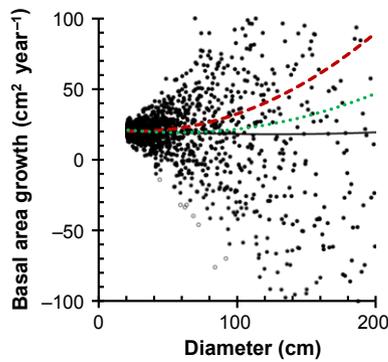


Fig. 2. Excluding even a small percentage of negative growth values can bias perceived patterns. Here, we use an example simulation illustrating how selective treatment of measurements generates an appearance of increasing basal area growth with stem size. Black circles are simulated growth measurements with errors; the black line shows a best-fit quadratic regression relationship for all data; the dashed line and the dotted line (red and green in the online version) show the best-fit quadratic regression relationship after filtering the lowest 5% and 1% of normally distributed growth measurements, respectively (white and grey filled circles excluded). In this simulation, ‘true’ basal area growth was held at $20 \text{ cm}^2 \text{ year}^{-1}$ and diameters are measured with normally distributed error.

error of confusing the characteristics of populations with those of individuals or subpopulations is sometimes called an ‘Ecological Fallacy’ in the social sciences with ‘ecological’ referring to sample data (Piantadosi, Byar & Green 1988; Pearl 2014). While often subtle in nature, such errors create a mismatch between a phenomenon of interest and the explanations for it, which can lead to a restricted or inadequate appraisal and a flawed understanding. Consider a population of imaginary trees where each grows at a constant but different rate. Now assume too that likelihood of death per unit time was equal and constant for all the stems: faster-growing trees will contribute an increasing proportion of (surviving) stems at larger sizes (Fig. 3). Thus, mortality alone would determine aggregated stem growth trends. The difference between individual and aggregate trends requires only that the relative likelihood of stems achieving a given size varies with individual growth. We provide a more sophisticated illustration with unimodal growth curves in the Supporting Information (see Appendix S1 and Fig. S1).

As a statistical generalization, most stems of most tree species die before they reach the very largest sizes: the exceptions have typically lived longer and/or grown faster than most others (Snyder & Ellner 2016). Thus, aggregate and individual growth-by-size patterns reflect distinct outcomes. Observations among forest trees indicate that the probability of death before reaching a given size is positively related to the time required to reach it and large trees have typically grown faster than average while at smaller sizes (see, e.g. Landis & Peart 2005; Rozendaal *et al.* 2010; Brienen, Gloor & Zuidema 2012). This effect is accentuated because slower-growing trees are typically at

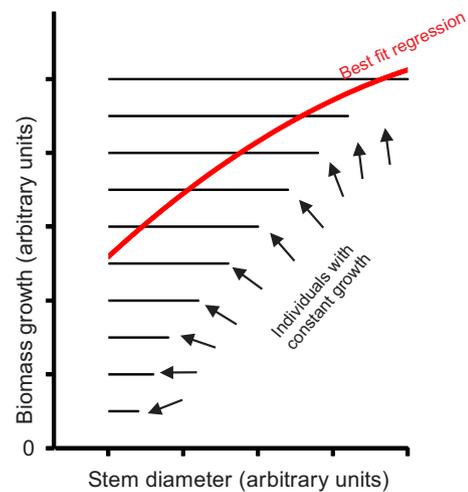


Fig. 3. Schematic illustration of how increasing mean biomass growth can arise with increasing size even when individual stems have constant growth. Black lines designate distinct stems (or subpopulations), and the line (red in the online version) shows a quadratic fit of the average biomass growth by stem size. In this imaginary example, slower-growing stems are a greater proportion of the total at smaller sizes and a lesser proportion at larger sizes.

increased risk of mortality per unit of time when compared to more vigorous stems (Vanclay 1994; Sheil 1995; Wyckoff & Clark 2002; Bigler & Bugmann 2004; Rüger *et al.* 2011) and relative differences in growth among stems can be sustained for decades (Kohyama & Hara 1989; Sheil 1995; Brienen, Zuidema & During 2006; Rozendaal & Zuidema 2011). Such differences will be further accentuated as smaller stems frequently suffer higher mortality than larger stems, for example during stand dynamics (Muller-Landau *et al.* 2006), as a result of damage from falling debris (Clark & Clark 1991), or due to predation by large animals (Sheil & Salim 2004) and the impacts of ground fires (van Nieuwstadt & Sheil 2005). In theory, a reversed trend could also occur if transition through a size class was more probable for slower- than for faster-growing stems. Such processes could perhaps occur when faster growth was a trade-off against low investment in roots, resulting in greater vulnerability to drought or to wind storms (Everham & Brokaw 1996; van Nieuwstadt & Sheil 2005; Webb *et al.* 2014; Bennett *et al.* 2015).

While differences in aggregate and individual-level growth patterns appear inevitable, it is less obvious whether a switch from increasing to decreasing biomass growth is likely. We thus decided to examine these relationships further.

MEASURED GROWTH TRAJECTORIES OF LARGE TREES

We reasoned that we could clarify and illustrate our concerns about the differences between aggregate and individual size–growth relationships by assessing the growth trajectories of individual trees. For this illustration, we used tree-ring measurements to analyse how biomass

growth trends vary with size within individuals and among stems for 14 species from three sites (see Table S1) with two generic diameter–biomass functions (Chave *et al.* 2005, 2014). We estimated growth in above-ground biomass using annual rings in 706 large individual trees: approximately 50 from each species. We sought 100 trees for each species, but only use the 50 largest individuals in the analyses presented here (see, Appendix S2 for additional details). Our primary analyses adapted the piecewise regression approach of Stephenson *et al.* (2014) to our data so as to assess biomass growth–size relations in two distinct ways: (i) individually and (ii) in aggregate.

Biomass growth trends within stems (individual-level)

We analysed growth trajectories for individual trees from estimated annual biomass growth. We then applied piecewise regressions for each individual, using 2, 3 or 4 linear segments. Segment breaks were determined by bootstrapping, and we only considered models with five or more data points (i.e. a period of 5 years of growth) per segment. For each stem, we selected the model with the lowest Akaike Information Criterion value (Akaike 1974; AIC see, e.g. Fig. S2). Therefore, the AIC determined the number of segments in the selected model. All analyses were conducted using R version 3.0.2 (R-Core-Team 2013). The piecewise regression models were fitted using the R-package *Segmented* (Muggeo 2003, 2008).

We noted the slope of the final section of the ‘best’ regression for each stem. For each of the 14 species in the individual-level analysis, the resulting slopes were almost equal proportions of positive and negative (see Fig. 4), with positive trends in 55.9% of all stems using biomass estimates from Chave *et al.* (2005; see Table 1). The median slope of nine of the 14 species was positive, but the 95% confidence interval of the median slope included zero in all but one of the 14 species. The Chave *et al.* (2014) biomass equation yielded similar figures (positive in 54.5% of stems and median slope positive in seven of 14 species). For two species, *Hura* and *Azelia*, the median slope of the last segment changed from positive to negative, but remained close to zero in each of these cases (Table 1). Thus, we detect no marked tendency towards increasing biomass growth among the largest individuals in our study species. An analogous analysis for basal area growth gave equivalent results, that is no indication that basal area growth shows any trend with size within individuals for any of our species.

To assess whether the largest stems in the study populations possessed a different tendency to the rest we also related the slope of the final section of the best regression for each species to diameter. We found a significantly decreasing slope in biomass growth for seven species (see Fig. 5). The negative slopes indicates that in half of our study species, the largest trees tend to have

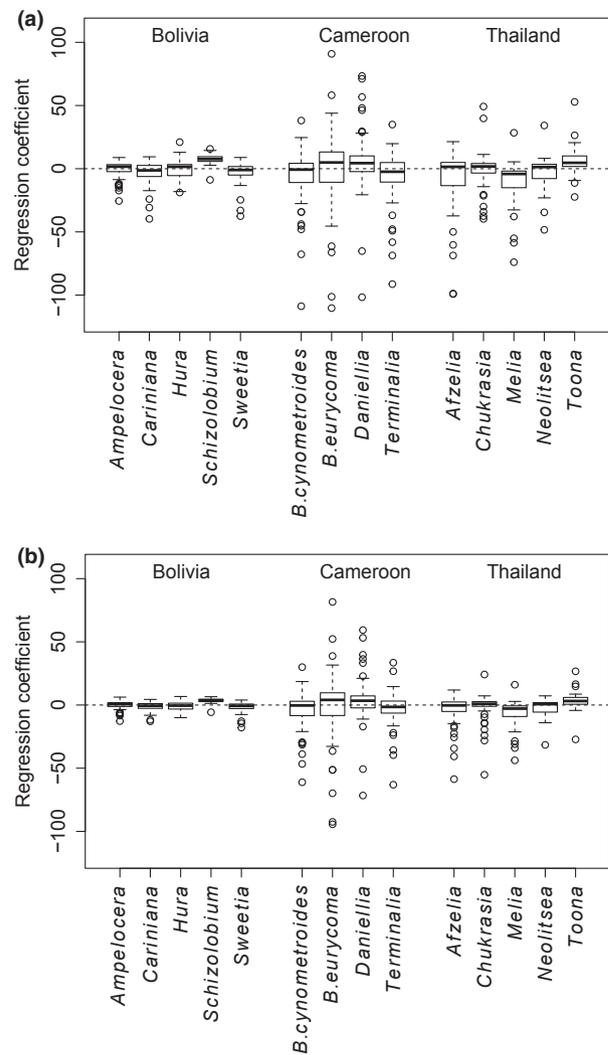


Fig. 4. Boxplot of the slopes of the last segment of the piecewise regression for the individual-level analysis for each species ($n = 706$ trees). Note that a few outliers ($n = 2$) were not shown for reasons of clarity. (a) Biomass estimates using Chave *et al.* (2005) and (b) biomass estimates using Chave *et al.* (2014).

more negative slopes than do those of somewhat smaller individuals.

Biomass growth patterns among stems (aggregate level)

To construct our aggregate-level assessment, we selected the last five growth rings per individual and calculated the mean annual biomass growth for these 5 years and again conducted a segmented regression approach for each species using only one growth value per stem. At the aggregate level, estimated biomass growth and size were positively related even among the largest trees for 13 of our 14 species with both biomass relationships (Fig. 6, Table 1). *Terminalia* was the exception and possessed the least consistent trend requiring four segments for the best-fit regression (Fig. 6i).

To summarize: at the aggregate level, we find that estimated biomass growth in larger stems generally appears greater than in smaller stems for most species, whereas at the individual level, such general trends are absent.

Discussion

Accurate assessments and interpretations of growth in the largest trees require precision and care. There are semantic problems: what is meant by 'the largest' trees, how is increased illumination with stature accounted for, and how are shorter- and longer-term declines in growth prior to death assessed. There are assessment challenges: representation, calibration, environmental influences and data quality controls all contribute uncertainties. There are analytical and inferential pitfalls: notably individual and aggregate trends are distinct and should not be confused. Accounting for every problem in every case remains challenging.

So are claims concerning biomass growth trends reliable? The problems we have described neither prove nor disprove that general biomass growth trends occur with size in populations or individuals, but each problem adds uncertainty. Our own analyses indicate that the long-presumed decline in biomass growth among large trees is hard to detect. Without long-term measurements and

suitable biomass calibrations, conclusions remain tentative, but growth patterns in at least some large stems appear to plateau for extended periods, with growth increases or declines subject to context.

Despite the widespread assumption that biomass growth ultimately declines at large stem size, studies providing clear evidence are scarce. One example is Piper & Fajardo (2011) who examined 10-year-diameter growth (derived from wood cores) for *Nothofagus pumilio* of various sizes at two sites in Chile. They found a marked rise-and-fall aggregate pattern in implied basal area growth with height (and inferred tree age) at both sites that appear sufficiently marked to indicate that biomass growth will almost certainly rise and fall although this is not demonstrated explicitly and trends for individual stems are not provided. Extended periods of relatively constant basal area growth with indications of an ultimate decline have been reported in large Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) though these observations have not been calibrated for biomass growth (Poage & Tappeiner 2002). Other studies that examine growth prior to death suggest a decline in biomass growth in individual stems is common and can be extended, but this has neither been assessed directly nor placed in a wider population context (Pedersen 1998). Despite the

Table 1. Results of the piecewise regression analysis for individual- and aggregate-level analysis using two biomass estimates (Chave *et al.* 2005 and Chave *et al.* 2014). Shown are the median slope coefficients of the last segment in the piecewise regression analysis and the total percentage of negative slopes for the individual-level analysis. Minimum d.b.h. of the last segment refers to the last breakpoint of the piecewise regression model, and slope coefficients for the piecewise regression analysis at the population level are shown

Country	Species	Biomass from Chave <i>et al.</i> (2005)				Biomass from Chave <i>et al.</i> (2014)			
		Individual-level results		Aggregate-level results		Individual-level results		Aggregate-level results	
		Median slope last segment piecewise regression	% negative slopes	Minimum dbh last segment	Slope of the last segment in the piecewise regression	Median slope last segment piecewise regression	% negative slopes	Minimum dbh last segment	Slope of the last segment in the piecewise regression
Bolivia	<i>Ampelocera ruizii</i>	1.66	38.3	18.71	3.17	0.68	42.6	18.71	1.48
	<i>Cariniana taneirensis</i>	-1.33	54.9	75.25	2.87	-0.58	54.9	74.77	1.27
	<i>Hura crepitans</i>	1.54	46.9	33.72	4.42	-0.48	53.1	33.72	1.49
	<i>Schizolobium amazonicum</i>	7.64	2.3	23.63	4.71	3.66	2.3	23.63	2.01
Cameroon	<i>Sweetia fruticosa</i>	-1.02	55.6	9.27	0.92	-0.68	63.0	9.27	0.38
	<i>Brachystegia cynometroides</i>	-0.71	55.7	45.43	4.36	-0.35	52.5	45.43	3.05
	<i>Brachystegia eurycoma</i>	4.93	39.7	93.28	10.45	4.05	34.9	63.91	5.52
	<i>Daniellia ogea</i>	4.40	28.8	61.89	6.50	3.42	30.8	61.89	4.10
	<i>Terminalia ivorensis</i>	-2.39	52.8	132.51	-7.86	-1.50	58.5	128.77	-4.34
	Thailand	<i>Afzelia xylocarpa</i>	1.50	47.1	92.86	9.17	-0.30	52.9	91.68
<i>Chukrasia tabularis</i>		1.80	41.5	53.71	0.43	0.95	34.0	54.25	0.01
<i>Melia azedarach</i>		-4.16	77.8	47.57	1.99	-2.84	77.8	47.57	0.96
<i>Neolitsea obtusifolia</i>		1.33	42.3	23.75	3.11	0.70	46.2	23.75	1.73
<i>Toona ciliata</i>		4.66	19.4	41.26	2.85	3.16	22.6	41.26	1.32

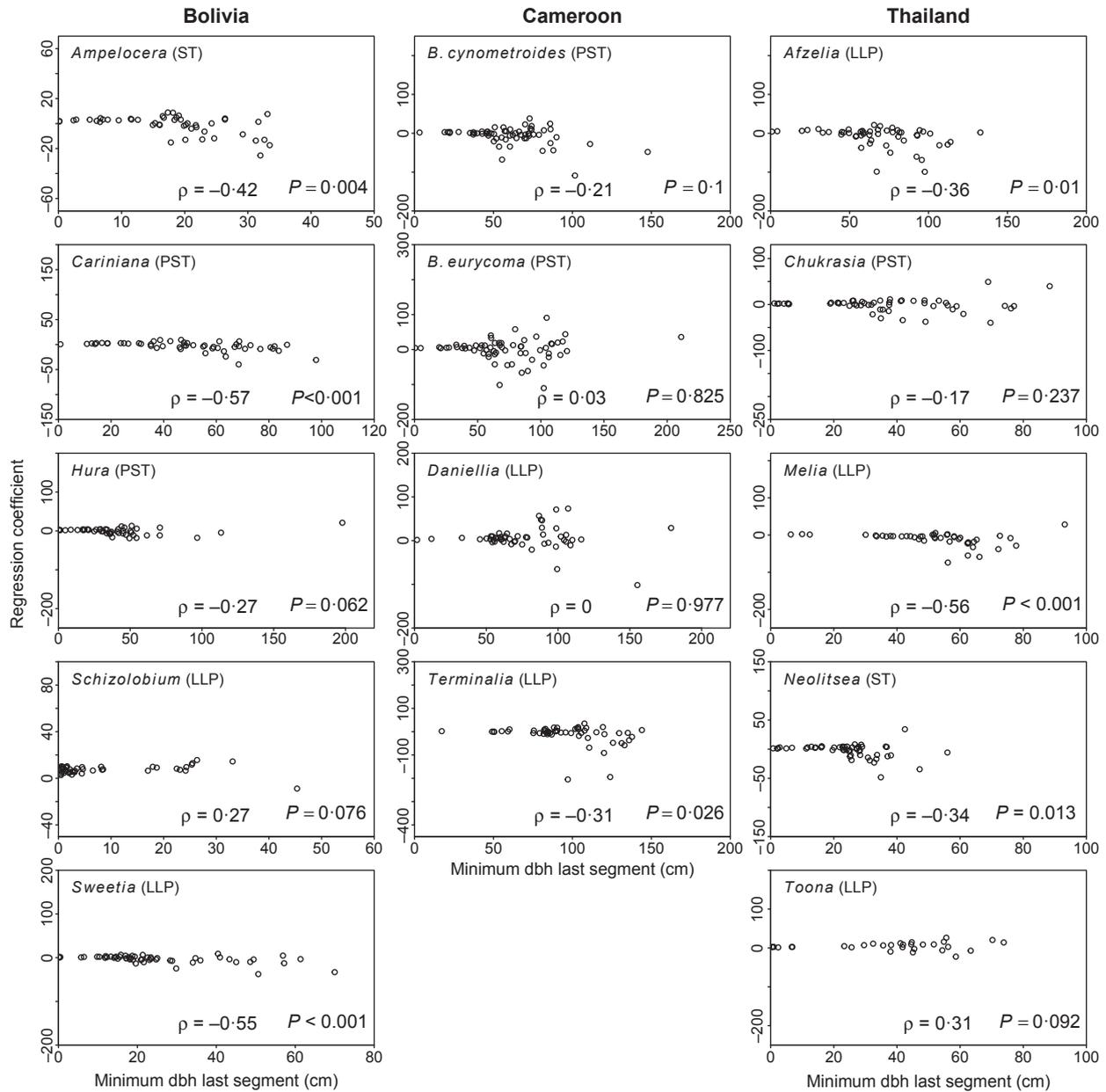


Fig. 5. Relations between regression coefficients of the last segment in the individual-level piecewise regression analyses and minimum tree size (d.b.h.) of the last segment. Note variation in Y scales. Spearman rank correlation rho (bottom)- and P-values (bottom right) are indicated in the panes. Species names are abbreviated to the genus and followed by letters indicating guild: ST, shade-tolerant; PST, partial shade-tolerant; LLP, long-lived pioneer. See Table S1 in the supporting material for details.

prevalence of the assumption that biomass growth ultimately declines at large tree sizes, we find no strong claims that this is generally true nor do we find concrete examples for either aggregate or individual trends.

In contrast to decreasing biomass growth, several data-rich studies have made specific claims about increasing biomass growth. Initially, the claims seem plausible, but as our review indicates, there is room for doubt and confusion. Despite appearing to focus on individual-level processes, all the current studies consider only aggregate (one value per stem) growth–size patterns. Trends within individual stems remain unaddressed and thus uncertain. So what about the aggregate patterns? For Sillett *et al.* (2010)

and Sillett *et al.* (2015), the use of multiple stem measures reduces some of our concerns about volume calibration but we remain uncertain about measurement errors and biomass estimates. Longer census intervals, accounting for stem turgor, and use of tree-ring data could all improve confidence. Increasing biomass growth in the world's largest tree species would not mean that these patterns are generally applicable to the largest individuals of other species. Although we also see an increase in growth with size among our stems (though not within them), our trees too are growing under intense competition and include few of the largest stems. Inadequate sampling, calibration and measurement may contribute to these results.

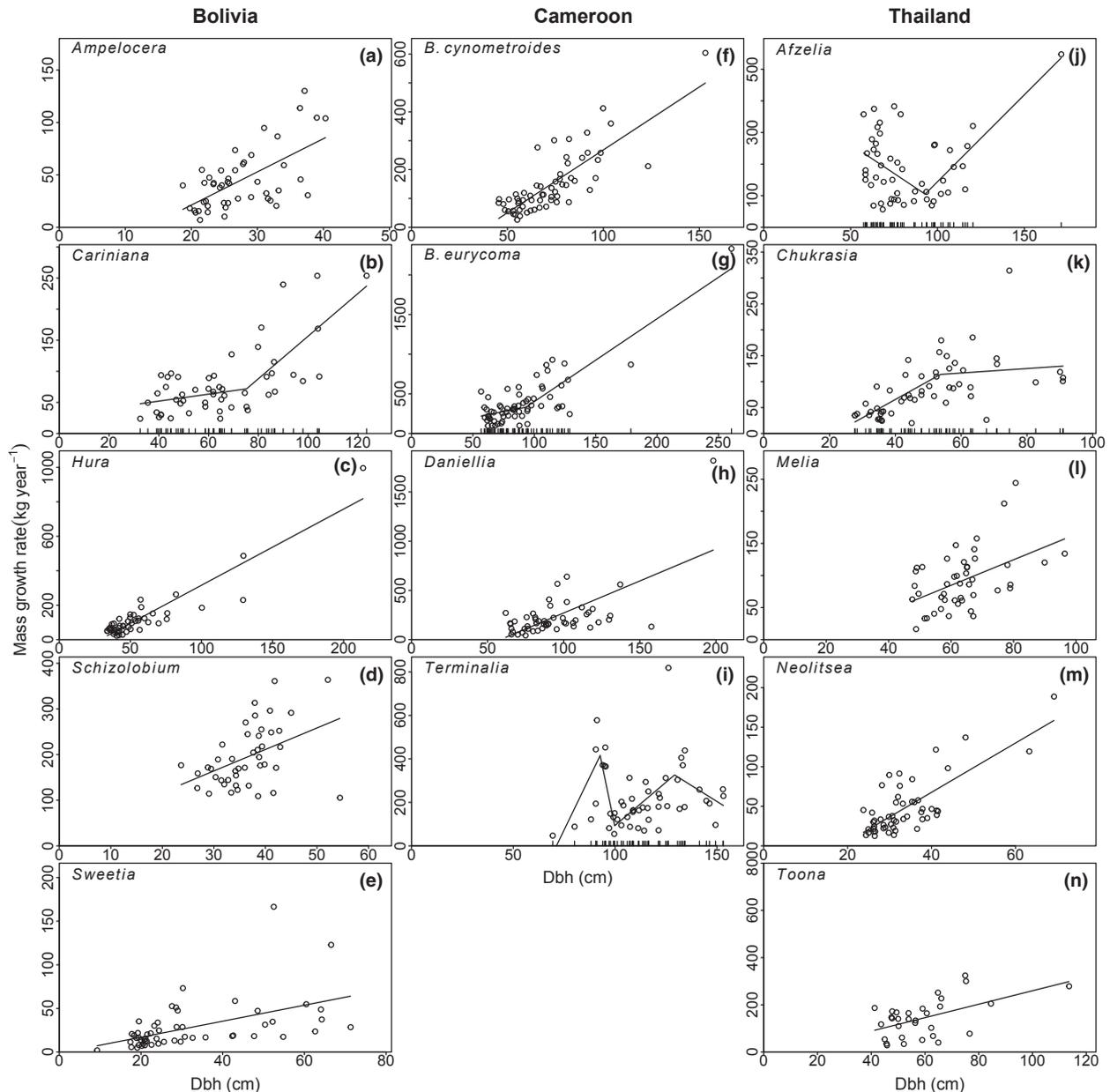


Fig. 6. Best-fit piecewise regression lines when we assessed biomass growth vs. stem diameter for the 14 study species at the aggregate level. Biomass growth was calculated over the 5-year period in the interval 2006–2010. Note variation in Y scale. Model selection was determined by the lowest value for the associated Akaike Information Criterion (AIC).

Stephenson *et al.* (2014)'s compilation of growth relationships for 41 tree species grown in open conditions merits attention because, as the authors acknowledge, all their other results (as with Sillett *et al.*'s) derive from forest stands and may simply reflect size-dependent competition. We note that the open-condition relationships are not a compilation of open-condition growth observations but derive from models using a fitted competition term which was set to zero for the purposes of simulating open growth. Furthermore, few large trees were used in developing these relationships, and several lack data points at even half the maximum diameter of the species in question. The form of the fitted relationship determines the implied

trends at large sizes. These relationships fall short of proving biomass growth increase at large sizes. More data concerning biomass growth in large open-grown trees are needed.

So what should researchers do? We need to stay objective. We need to understand and assess errors and uncertainties as alternative explanations of any observed patterns. Whatever trends are detected, whether in individuals or in aggregate, we need to be able to determine how selection, measurement and estimation procedures and their associated errors, biases and calibration uncertainties may have contributed. We need robust observations and analyses to permit the inferences required. We must

distinguish individual and aggregate properties and highlight when they may be confused.

Tree growth can be assessed in different ways. Each has limitations: that is, repeated measurements (Ganghofer 1881; Vanclay 1991; Sheil 1995, 2003; Chitra-Tarak *et al.* 2015); dendrometers (Reineke 1932; Hall 1944; Keeland & Sharitz 1993; Sheil 2003); and growth rings (von Guttenberg 1896; Brienen, Gloor & Zuidema 2012; Nehrbass-Ahles *et al.* 2014; Peters *et al.* 2015). When repeated measurements are used, we encourage long intervals or multiple measurements in series. Measurements implying negative growth should not be discarded, but all measurements, checks and corrections should be recorded and archived. Cross-validation through multiple approaches could improve confidence in results and conclusions. Dendrometers are reserved for short-term studies and can be used to help correct for turgor effects (Sheil 2003; Chitra-Tarak *et al.* 2015). For longer-term assessments of trends, simultaneous characterization of individual-based (tree ring derived) and population-based (plot- and stem-measure based) growth at the same sites would be valuable.

Further work on tree rings allows evaluation of individual diameter and volume growth at multiple locations over each tree's life span (in open-grown as well as closed forest conditions). Challenges for those using tree-ring data to address biomass growth in the tropics include (i) the limited availability of data, (ii) the lack of distinct rings in some species, (iii) the rarity of suitable trees, (iv) the unavailability of such trees for destructive sampling, (v) the need for calibrated size–biomass relationships, and (vi) the need to separate environmental influences and developmental changes. We recommend that existing tree-ring data should be compiled, shared and assessed, sampling methods and trend analyses can be further developed, and procedures can be set up to ensure large trees are identified and prepared for their detailed analysis when they die.

Whatever growth data we work with, calibrations must be adequate for the populations and resulting inferences under consideration. A major research programme is required to provide accurate size–biomass relationships for study populations.

Development and wider application of alternative techniques may reduce specific uncertainties. For example, terrestrial laser scanning may help assess volume (Calders *et al.* 2015; Hess *et al.* 2015), while drilling (Rinn, Schweingruber & Schär 1996) and other non-destructive methods can help assess wood density patterns (Nicolotti & Miglietta 1998; Leong, Burcham & Fong 2012). Much remains to be done in the study of large trees. Energy capture, growth efficiency and form change merit further assessment. Population data on stem damage, rot and pre-death behaviours are also urgently required.

Conclusions

The biomass growth trends of the largest individual trees remain uncertain. We highlight challenges and suggest

how they may be solved, avoided or minimized. To claim general size-related growth patterns and trends among and within the largest stems requires clear results from the study of representative populations of the largest stems, careful treatment of exogenous influences, approaches to reduce and account for biased measurements, suitable size–biomass calibrations, and avoidance of statistical pitfalls and logical errors. Inferences about growth trends in individual stems require assessments of individual stems across multiple periods of growth. Individual and aggregate properties need to be consistently distinguished. The increasing availability of long-term repeated observations and tree-ring measurements will facilitate and encourage the assessment of long-term trends. We must strive to ensure these efforts are as reliable as possible.

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Data accessibility

Data are deposited in the Dryad Data Repository <http://dx.doi.org/10.5061/dryad.22vg4> (Sheil *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. The ecological fallacy in growth curves.

Appendix S2. Tree ring data used to compare individual and aggregate patterns.

Fig. S1. Example of a family of curves where $Y = X^a - 0.02 X$ (thin lines).

Fig. S2. Three examples of annual biomass growth vs. stem diameter for individual trees based on growth rings.

Table S1. Characteristics of the 14 study species; their shade-tolerance guild (ST, shade-tolerant; PST, partial shade-tolerant; LLP, long-lived pioneer); wood density, as used in the equations used to estimate biomass growth; total number of trees and diameter range of the trees included in the analysis.