Biogeosciences, 14, 4663–4690, 2017
https://doi.org/10.5194/bg-14-4663-2017

Biogeosciences Open Access

Reviews and syntheses: Field data to benchmark the carbon cycle models for tropical forests

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Received: 30 April 2017 – Discussion started: 5 May 2017
Revised: 19 August 2017 – Accepted: 8 September 2017 – Published: 23 October 2017

Abstract. For more accurate projections of both the global carbon (C) cycle and the changing climate, a critical current need is to improve the representation of tropical forests in Earth system models. Tropical forests exchange more C, energy, and water with the atmosphere than any other class of land ecosystems. Further, tropical-forest C cycling is likely responding to the rapid global warming, intensifying water stress, and increasing atmospheric CO_2 levels. Projections of the future C balance of the tropics vary widely among global models. A current effort of the modeling community, the ILAMB (International Land Model Benchmarking) project, is to compile robust observations that can be used to improve the accuracy and realism of the land models for all major biomes. Our goal with this paper is to identify field observations of tropical-forest ecosystem C stocks and fluxes, and of their long-term trends and climatic and CO_2 sensitivities, that can serve this effort. We propose criteria for reference-level field data from this biome and present a set of documented examples from old-growth lowland tropical forests. We offer these as a starting point towards the goal of a regularly updated consensus set of benchmark field observations of C cycling in tropical forests.

1 Introduction

> The near-future research effort should be on development of a set of widely acceptable benchmarks that can be used to objectively, effectively, and reliably evaluate fundamental properties of land models to improve their prediction performance skills. (Luo et al., 2012).

Improved modeling of tropical-forest carbon (C) cycling is urgently needed for projecting future climate and for guiding global policy concerning greenhouse gases. Tropical forests are major players in the global C cycle. These ecosystems store an estimated 25 % of terrestrial C stocks (Bonan et al., 2008), they exchange vast quantities of carbon dioxide (CO_2) with the atmosphere (Beer et al., 2010), and their C cycling is climatically sensitive (Clark et al., 2003, 2013; Balser and

Wixon, 2009; Wood et al., 2012). Atmospheric inverse models indicate that temperature-linked changes in the annual C balance of the land tropics during recent decades (higher tropical emissions in hotter years) have largely driven the marked inter-year changes in the growth rate of atmospheric CO_2 ([CO_2]), after factoring out fossil fuel emissions (Ciais et al., 2013; also Anderegg et al., 2015).

In addition to the ongoing effects of deforestation and fires, climate change is likely to magnify the biome's large role in global C cycling. Tropical forests are being rapidly moved into new climate territory (Wright et al., 2009). One Earth system model (ESM) has projected that, during the next 25 years, up to 70 % of seasons in the tropics will be hotter than all the corresponding seasons before 2000 (Diffenbaugh and Scherer, 2011). While future tropical rainfall regimes remain highly uncertain (Collins et al., 2013), it is clear that warming also progressively increases relative air dryness (vapor pressure deficit, VPD; Sherwood and Fu, 2014), placing another downward pressure on tropical-forest productivity (Clark et al., 2013). Although some ecophysiological theory indicates that increasing [CO_2] could mitigate these stresses (Lloyd and Farquhar, 2008), such "CO_2 fertilization" for tropical forests is expected to be constrained by widespread nutrient limitation (Townsend et al., 2011; Goll et al., 2012; Wieder et al., 2015) and is also likely to be offset by the increasingly negative effects of climate change across the tropics (Wood et al., 2012; Clark et al., 2013; Smith et al., 2016). The net effect of all these environmental factors will strongly affect how this biome contributes to, or detracts from, the land C sink in coming decades, with large consequences for the pace of global warming.

Projecting the future integrated effects of climatic and atmospheric change on tropical forest C cycling can only be approached through process-based modeling. Current models, however, strongly disagree among themselves with respect to tropical forests, thus producing major uncertainties for global diagnosis and planning. While some coupled ESMs indicate increasing net C uptake by the land tropics through this century, others project a progressive decline in the net flux, with the spanned difference approaching 7 $\mathrm{Pg\,C\,yr^{-1}}$ by 2100 (Fig. 1). Multiple studies (Delbart et al., 2010; Negrón-Juárez et al., 2015) have reported large mismatches between spatially referenced ground observations (tropical-forest aboveground biomass, woody productivity, tree mortality) and the corresponding outputs from ESMs in the CMIP5 studies (Coupled Model Intercomparison Project, Phase 5). A further indication of unresolved issues for modeling this biome is that 9 of 10 C cycle models failed to simulate the climatic responses of the global land C sink through 1980–2009 as inferred from the atmospheric data (most models overestimated the land sink's sensitivity to rainfall and/or underestimated its sensitivity to temperature; Fig. 6.17 in Ciais et al., 2013).

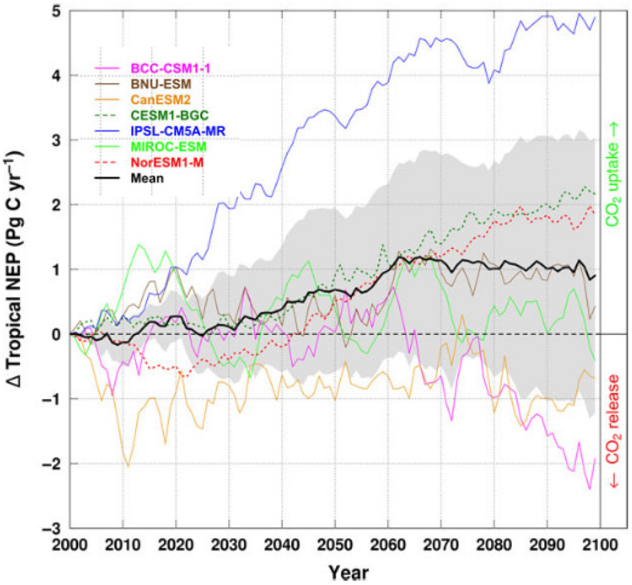

Figure 1. Divergent projections (colored lines) of the changes in tropical net ecosystem production through this century from seven of the CMIP5 climate models. The key identifies the models. Dashed lines: models that include coupled carbon–nitrogen (C–N) biogeochemistry; solid lines: models lacking explicit nutrient cycling. The ensemble mean is indicated by the heavy black line, and gray shading indicates the range of 1 standard deviation (1δ) in climate model variability (adopted with permission from Cavaleri et al., 2015, © 2015 John Wiley & Sons Ltd).

To improve current global C cycle models, a community-wide effort – ILAMB (the International Land Model Benchmarking project) – seeks to identify robust observations from each biome (hereafter, "benchmark data") that can serve to guide model structure and to enable standardized tests of the models (Luo et al., 2012). Our goal with this paper is to contribute to the ILAMB effort by identifying such reference-level field observations from tropical forests to guide the models for this biome. We restrict our focus to the most extensive and most C-rich sector of the biome (Raich et al., 2006): old-growth forests in the tropical lowlands (elevations < 500 m). Given the large footprint of global models (e.g., kilometer scale), we additionally focus specifically on larger-scale, landscape-level ecosystem fluxes and pools rather than on data required for refining functions and relationships within models. While we recognize the need to incorporate nutrient cycling into global models, we limit our focus to carbon, although the criteria used here could be applied to nutrient fluxes and pools as well. We first propose criteria for identifying benchmark-level field observations from these forests. We then review the current availability of such data and present a set of documented examples. We offer these ideas and examples as a starting point towards the goal of a constantly updated consensus set of benchmark field observations for the tropical-forest biome.

2 Types of model–data interactions

Field observations from tropical forests can help develop and validate models in multiple ways. First, for each C cycle model, the prescribed and diagnostic ecosystem metrics for the biome should be comparable to the relevant field data. For instance, do the modeled leaf area index (LAI), aboveground live biomass, and aboveground wood production fall within the 95 % confidence limits of the observations from tropical forests? Do relationships among stocks and fluxes match the relationships found among the field observations? Such questions can be posed at the biome level or for specific tropical regions, depending on a model's spatial resolution and the available data. The pattern of spatial variation in model outputs for different tropical-forest regions can be tested against the field observations (e.g., Negrón-Juárez et al., 2015). Observations from tropical-forest field sites can also be used to evaluate the results from site-specific model experiments for the years spanned by those field studies. Do the modeled C stocks and ecosystem responses and their interannual variation approximate the observations for the corresponding time period? For all these uses, multiple issues arise for selecting and using appropriate field data, and we discuss these individually in the following sections.

A fundamental consideration for model–data interactions is comparing "apples to apples." The field studies to date in tropical forests have addressed only some of the forest attributes and processes involved in C cycling. As also discussed by Cleveland et al. (2015), considerable uncertainty is introduced when model structure and results are compared to C cycle estimates that are only partially based on field observations (henceforth termed "hybrid estimates"). Figure 2 is from an example study comparing such hybrid estimates to results from C cycle models. The first-cut C cycle estimates of Malhi et al. (2009) had been derived by combining the available field observations for some C cycle aspects with unverifiable estimates for unmeasured components such as daytime leaf respiration and coarse-root biomass. Other aspects that were omitted may be important in most tropical forests. These include the large CO_2 flux from canopy-level branches (Cavaleri et al., 2006) and the summed belowground C exports to mycorrhizae and root exudates. Similarly, in a high-profile study (Pan et al., 2011) the net C balance of intact tropical forests was estimated based on field-estimated change in aboveground tree biomass in study plots and on the assumptions that all other biomass components (e.g., belowground biomass) changed at the same rate as aboveground tree biomass and that soil carbon did not change. These hybrid C balance estimates were then used by Schimel et al. (2015) to evaluate TRENDY models. While there can be considerable heuristic value in partially biometric estimates for C stocks and fluxes, they do not provide direct observational standards for the models. The most robust comparisons of models with field data will be for those specific pools and fluxes that were assessed in the field.

The other side of the apples-to-apples issue is that, for data–model comparisons, many C cycle models may require development to include or output those specific ecosystem attributes that have been field-quantified in tropical forests (e.g., aboveground wood production, leaf litterfall). Similarly, the land surface models may need to be restructured to better represent properties for which only part of the system state can actually be observed (e.g., predicting surface-soil organic C (SOC), rather than total-column SOC; cf., Koven et al., 2013).

Two further aspects will determine the usefulness of data–model comparisons. One is the need for the field researchers to clearly communicate the underlying methods and their limitations. The other is that the modelers carefully evaluate field-based observations and take into account their limitations for use in model–data exercises.

3 Criteria for benchmark field data from tropical forests

3.1 Direct field measurements

As discussed above, some reported observations of C cycle attributes are based partly on direct measurements and partly on extrapolation. An example would be total fine-root production as estimated by extrapolating surface-soil measurements to the unstudied deeper soil layers (e.g., Doughty et al., 2014). Similarly, the tower-based eddy covariance technique measures forest-level net ecosystem exchange (NEE) of CO_2. Because this technique does not measure the two component fluxes of NEE, gross primary productivity (GPP) and ecosystem respiration (R_{eco}), modeling and assumed physiological responses have been used to infer those two fluxes from NEE (Wehr et al., 2016). As recently argued by Negrón-Juárez et al. (2015), the most meaningful model–data comparisons will be those based as closely as possible on the actual field measurements (i.e., surface-soil fine-root production and NEE in the examples above). Because the current field techniques all have clear limitations (Clark et al., 2001a; Cleveland et al., 2015), such observation benchmarks also need to be explicitly associated with the specific method used. If a superior method emerges, those benchmarks would need updating.

3.2 Landscape-scale data

> Field measurements can be comparable to the predictions of global NPP models (and could be eventually used for parameterizing them) only when they are collected by a systematic stratified design, and are therefore representative of the given region. (Simova and Storch, 2016)

> … extrapolations and predictions of forest properties based on sparsely and/or non-randomly dis-

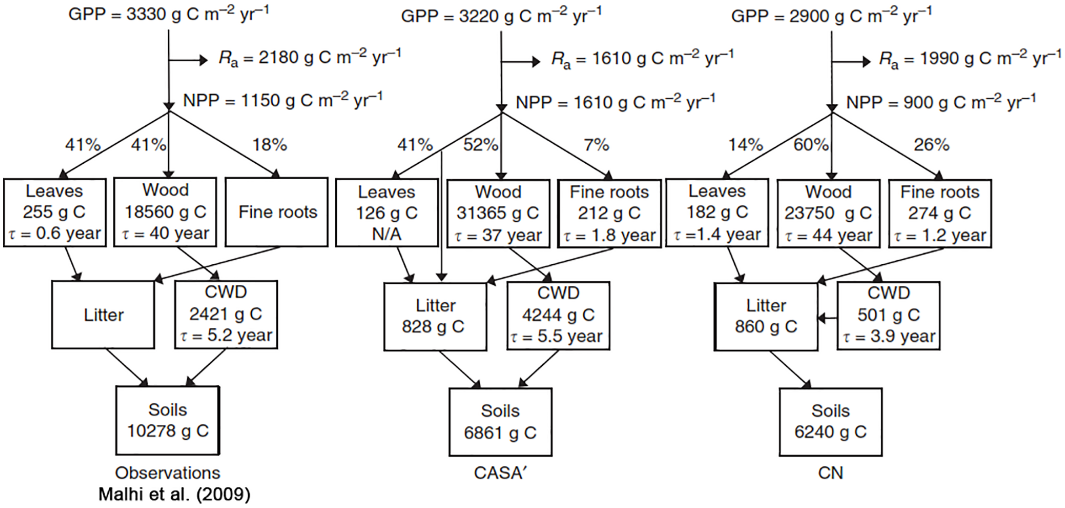

Figure 2. A comparison of CASA and CN model outputs to estimates derived by combining the limited field data with estimates of unmeasured components (from Randerson et al., 2009, with permission from © 2009 Blackwell Publishing Ltd.).

> tributed field plots are no longer acceptable for understanding tropical forests in regional or global carbon cycles. (Marvin et al., 2014)

> A single plot corresponds to one sample of the forest, and it is unlikely to represent the whole landscape-scale environmental variability. (Chave et al., 2004)

Many key features of C cycling (e.g., C stocks, LAI, productivity) vary within each tropical forest due to the local-scale variation in disturbance histories, edaphic conditions (slope, fertility) and floristics. Indeed, in landscapes that can support hundreds of tree species per hectare (Losos and Leigh, 2004), the potential for small-scale variability in plant properties, soil characteristics and thus C cycle attributes is very high. For example, among 18 0.5 ha plots distributed across a Costa Rican old-growth forest, estimated aboveground wood production varied 2-fold (Clark et al., 2013) and the large mortality-driven biomass losses occurred in only a few of the 18 plots (Clark, 2004).

Most land surface models attempt to predict landscape-scale fluxes and pools. Field studies should therefore provide distributed measurements that span the within-landscape variability. When a forest is instead sampled in only one or two small ($\leq$ 1 ha) plots, as is the case for most sites covered by two current plot networks (RAINFOR in the Amazon, Brienen et al., 2015; AFRITRON in Africa, Lewis et al., 2009), the observations may be unrepresentative of average conditions in those forests. Using remote sensing over Peruvian tropical forests, Marvin et al. (2014) found that the structural attributes of individual small study plots significantly differed from the landscape-level mean attributes of each sampled forest.

For typical land surface models, which operate on a scale of 0.5° or larger, benchmark field observations would ideally be based on field measurements distributed over those extremely large areas. Due to both cost and the challenging logistics, however, no field study of ecosystem-level C cycling has covered such a huge area of tropical forest. Current consensus (e.g., Chave et al., 2004; Rutishauser et al., 2010; Chambers et al., 2013; Marvin et al., 2014) favors two compromise approaches to representative sampling of a tropical-forest landscape for such studies: (1) measurements over a set of small plots that aggregate to at least 5–10 ha and are distributed to span the important heterogeneity of the studied landscape (e.g., de Castilho et al., 2010; Rutishauser et al., 2010; Clark et al., 2013), or (2) measurements covering a very large plot, such as the 50 ha plots of the Center for Tropical Field Science (CTFS; Anderson-Teixeira et al., 2015). While these prescriptions do not achieve sampling on the scales treated in many ESMs, these compromise landscape-scale sampling approaches can be used to determine the ranges and means of C stocks and fluxes on the mesoscale (e.g., 50–2000 ha).

Two classes of models contrast with the ESMs in explicitly representing the small-scale within-landscape heterogeneity caused by the patchwork of disturbance and recovery phases observed in the real world. Demographic models such as the Ecosystem Demography model (Moorcroft et al., 2001; Medvigy et al., 2009; Fisher et al., 2015) are designed in part to capture the variation between recently disturbed and old-growth forests. Similarly, individual-based models such as TFS and LPJ-GUESS (Fyllas et al., 2014; Pappas et al., 2015) explicitly represent the within-landscape spatial heterogeneity. With those models the smaller-scale observations, such as those from individual hectares, can be usefully compared directly to the model output.

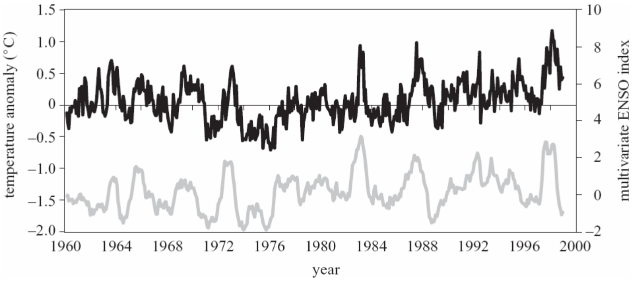

Figure 3. Anomalies of pantropical mean temperature (black) and the ENSO multivariate index (gray) compared to the period of 1960–1990. (from Malhi and Wright, 2004, by permission of the Royal Society).

3.3 Long data series

Key outputs from the global models concern the long-term trends in C cycle attributes in each biome due to both climate change and increasing atmospheric [CO_2]. Field-based reference benchmarks concerning either directional trends through time or the climatic and/or [CO_2] sensitivities of forest C cycling are needed to evaluate this aspect of model outputs. Such observational benchmarks need to be based on long data series. A two-sample comparison, then vs. now (e.g., Lewis et al., 2004), can be consistent with a hypothesized or modeled long-term trend but is insufficient to demonstrate or quantify it. With random draws of two observations from a time series that has no underlying significant temporal trend, on average in half the cases the second observation will be greater than the first. As demonstrated by Hall et al. (1998; also Clark and Clark, 2011), for the many tropical-forest processes and attributes that vary substantially among years, short data series are insufficient for reliable detection of long-term declines or increases.

When a long data series does exist for a given C cycle attribute or process, climatic and/or [CO_2] sensitivities of that aspect of forest C cycling can be quantified by statistically relating the observations to the changes in the environmental drivers. The interannual variation in tropical climatic conditions (Fig. 3) greatly aids such analyses. Valid climatic/[CO_2] relationships of C cycle attributes will increase in statistical significance as more yearly points are added (see Table 3 in Clark et al., 2013). Too-short data series, however, can miss the underlying climatic and/or [CO_2] responses or suggest spurious ones. For annual wood production in one tropical forest, in a retrospective analysis based on progressively shorter segments of a 24-year record (Fig. 4), many series of < 10 annual remeasurements missed the highly significant negative temperature response that was shown by the full record; some 6-year series in fact suggested the opposite, likely due to variation that was not controlled for in other climatic drivers. Ideally, modeling analyses should aim to capture the dominant causes of this interannual variability, where they are non-random. Again, apple-to-apple comparison is critical. It is necessary to look at the results in the context of local conditions and meteorology, rather than abstracting to larger scales.

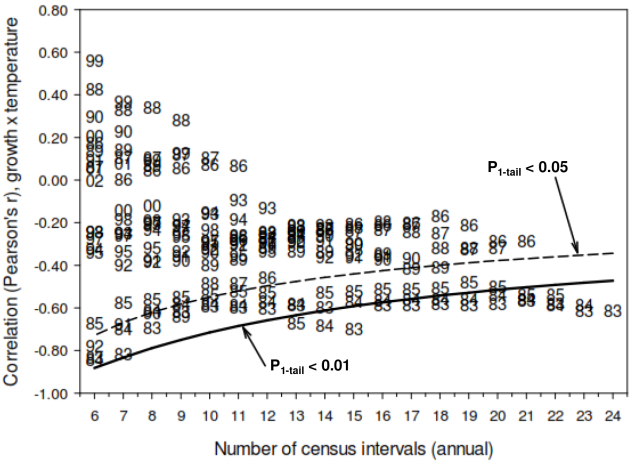

Figure 4. Effect of length of data series on the correlation of tree growth with minimum temperatures at La Selva, Costa Rica. Data labels: year 1 of each segment of the series (from Clark and Clark, 2011, with permission from the Association for Tropical Biology and Conservation).

3.4 Supporting information

For model–data fusion, benchmark field data should be accompanied by several classes of supporting information. Geographic coordinates of the study site are required for spatially explicit model tests. Site elevation (meters above sea level) locates the finding along the lowland-montane continuum of tropical forests. Given the likelihood of interannual and directional changes in forest C cycling, the year(s) of each study (often also the months) is critical information. Other key specifications include the area sampled, details of the field methods used, and the citation of the study. The web location of the actual data should also be part of each benchmark listing; although this last specification cannot yet be fulfilled for most tropical-forest field data, changes now underway in publication requirements may soon make this a realistic addition to the database design.

Ideally, model runs should be set up for individual test bed sites to best allow consideration of site-specific circumstances. Where these types of model–data fusion are planned, a much larger set of auxiliary data, including high-resolution local meteorological data, soil physical properties (texture, depth), and vegetation properties relevant to the question being posed, is potentially useful.

4 Benchmark field data from lowland old-growth tropical forests

Using the criteria above (direct field measurements, landscape-scale sampling, sufficiently long data series), we have extracted, from the literature, examples of robust ecosystem-level field observations of C cycling in these forests (Tables 1–13). Not surprisingly we found important data gaps. We also identified significant method issues for field-quantifying C cycle attributes. As discussed below, while some of these issues affect C cycle studies in all forest types, others are particular to tropical-forest conditions. In the following sections, for each C cycle attribute we review the state of the existing field data and present documented examples of robust field observations, when available. Two areas are specified in the example tables: the summed area of the actual measurements (e.g., cores, traps) and the total area of the forest over which the measurements were distributed (total study area: the area of a polygon encompassing all measurements). Table 14 provides core information on each study site in the preceding data tables.

Table 1 provides a capsule summary of our findings, which are detailed in the following sections. As illustrated in the table, C cycle attributes vary across space and/or time. Model predictions are typically for a single state in a given place and time. Increasingly, however, model predictions are made across a range of parameters (Zaehle et al., 2005; Fischer et al., 2011), initial conditions (Lombardozzi et al., 2014), driving data (Fox et al., 2009; Viskari et al., 2015), and structural variations (Fisher et al., 2015; Medlyn et al., 2015), resulting in ranges of predictions that can be compared against observations, which themselves are known to have errors. Therefore, it is not strictly necessary that observational benchmarks have very low confidence ranges, but it is necessary to document that range of observations and the natural variability that the observations span.

4.1 Leaf area index (LAI)

Field observations for this often prognostic model parameter are method-dependent and typically underestimate (see Table 2). Forest-level LAI can be assessed in the field directly, if laboriously, through replicated leaf harvests from the canopy top to the forest floor. To date, however, only one study (Clark et al., 2008) has directly assessed it this way in a tropical forest (LS site, Table 2). Harvested LAI at the 55 $4.6\,\mathrm{m}^2$ stratified random sampling points across that forest ranged from 1.2 to 12.9, reflecting the spatial heterogeneity of tropical-forest LAI and thus the need for distributed replicate sampling. Parallel estimates were also made with the two indirect techniques (LAI-2000, hemispherical photographs) that are the standard current approaches for estimating LAI in the field. Both indirect methods were found to saturate in sites of overhead $\mathrm{LAI} > 6$, resulting in 12–38 % underestimates of the direct harvest data, depending on the adjustments made for wood and/or leaf clumping (Olivas et al., 2013). In one other study involving direct harvest of all leaves from the forest floor to the canopy top in a $20\,\mathrm{m} \times 20\,\mathrm{m}$ plot (McWilliam et al., 1993; see Table 2), the value obtained was similarly at the high end of tropical-forest LAI observations.

4.2 Ecosystem C stocks

The total ecosystem C inventory has not been quantified in any tropical forest. Field-quantifying this C cycle attribute would be challenging for any forest type. Impediments in tropical forests include difficulty of access, harsh climatic conditions, marked within-forest variation, and the complex forest structure. Most frequently estimated in this biome is the aboveground biomass of the larger live woody stems. Components of live biomass that are as yet unquantified at the stand level in these forests include coarse roots, subsurface fine roots, epiphytes, hemiepiphytes, and understory plants. Coarse woody debris (CWD) is rarely estimated. When SOC is assessed, sampling is nearly always confined to the surface soil. For modeling, the available data from tropical forests provide a lower bound on total C stocks. These data are most valuable, however, at the level of individual components.

4.2.1 Live aboveground biomass

All field observations of live aboveground biomass in tropical (and nontropical) forests are indirect, un-validated estimates for just the larger stems (EAB, estimated aboveground biomass). For multiple reasons (see below), it remains unclear how the existing EAB values for this biome can best serve the models.

To derive EAB, all live stems in a stand above some diameter limit (usually 10 cm) are measured for diameter (rarely also height). Each stem's aboveground biomass is then estimated using an allometric relationship between biomass and diameter (sometimes also height) that was derived by harvesting and weighing individual trees at another site(s). This approach raises the issue of "... misplaced concreteness" with respect to forest biomass estimates (Clark and Kellner, 2012). Different allometric equations can produce starkly different values of EAB from the same set of stem measurements; this is illustrated in Table 3 by the range of the five estimates ($242–428\,\mathrm{Mg\,ha^{-1}}$) produced by different allometries but from the same 1992 set of tree diameter inventory data at the NOU-PP site. To determine which, if any, of such estimates is accurate for a given landscape would have required structured follow-up harvests at the site to test the applicability of a given allometric relation to that forest (Clark and Kellner, 2012). Because as yet no such validation has been carried out in a tropical forest, all EAB values for this biome are highly uncertain at the site level. While the range of these estimates is the only available guidance for

Table 1. Summary of the characteristics of field observations of ecosystem C cycling in lowland old-growth tropical forests, from the example data presented in this paper (in the tables or text, or footnotes here). n.d.: no benchmark field observations yet identified from this biome. Attribute abbreviations are defined in the text.

C cycle attribute	Range of forest-level means	Min/max a good indicator of lower or upper bound:	Within-site variation (ratio: max to min) at example sites:		Salient issues for attribute in tropical forests
			Ha to ha	Yr to yr	
LAI (full canopy)	4–6	Both bounds[a]			The two direct harvests indicate max. LAI ca. 6; optical methods underestimate
Ecosystem C stocks					
Total C stocks	n.d.				Unquantified components could sum to $>$ 50 % of total C stocks
Aboveground live biomass	161–497 Mg ha^{-1}		2.4	1.0–1.06	Estimates are typically for larger stems and are based on unverified allometry
Coarse roots	n.d.				No stand-level field observations
Fine roots	$>$ 0.5–8.0 Mg ha^{-1}	Lower bound	1.2–1.4	3.75[b]	Data are confined to surface soil
Coarse woody debris	20–96 Mg ha^{-1}				Few landscape-scale data; highly variable in space and time
Soil organic C	$>$ 213–373 Mg C ha^{-1}	Lower bound	1.75[c]		Almost never quantified to maximum soil depth or through time
Ecosystem C fluxes					
Annual NEE of CO$_2$	n.d.				Issues for eddy flux in tropical forests make annual NEE problematic (see below)
GPP	n.d.				Biometric omissions could sum to $>$ 50 %; GPP is not measured by eddy flux
R_a, R_h	n.d.				Field observations in tropical forests are incomplete and ambiguous (see below)
Total NPP	n.d.				Biometric omissions could sum to $>$ 50 %; total NPP is not measured by eddy flux
Aboveground wood production	3.7–8.7 Mg ha^{-1} yr^{-1}		1.4–2.1[d]	1.4[e]	Usually only larger stems ($\geq$ 10–35 cm diameter); based on unverified allometry
Mortality biomass loss	5.0–8.0 Mg ha^{-1} yr^{-1}		2.5-15.0	2.9	Marked spatiotemporal variation; based on unverified allometry
Leaf production	n.d.				No stand-level observations
Leaf litterfall	$>$ 5.7–6.8 Mg ha^{-1} yr^{-1}	Lower bound	1.6–2.2[d]	1.2[e]	Always an underestimate; excludes pre-collection losses (see Table 7)
Twig litterfall	$>$ 0.9–2.5 Mg ha^{-1} yr^{-1}	Lower bound	2.7–8.7[d]	1.5[e]	Always an underestimate; excludes pre-collection losses (see Table 7)
Reproductive litterfall	$>$ 0.4–1.3 Mg ha^{-1} yr^{-1}	Lower bound	2.5–6.4[d]	1.4[e]	Always a strong underestimate; excludes consumption
Fine-root production	$>$ 0.7–3.4 Mg ha^{-1} yr^{-1}	Lower bound			Only in surface soil; significant method issues
Plant C exports to symbionts	n.d.				Unquantified; possibly a nontrivial and/or increasing NPP fraction
Root exudates	n.d.				Unquantified; possibly a nontrivial and/or increasing NPP fraction
Volatile organics production	n.d.				Unquantified in tropical forest; likely a small but increasing fraction of NPP

[a] Minimum from indirect methods likely a good indicator of lower bound of LAI; 6 is a reasonable upper bound (but based on only two harvest studies).
[b] Ratio between the 8-year maximum and 8-year minimum of stocks of live fine roots ($<$ 2 mm, 0–50 cm depth) in old Oxisols; LS site (Espeleta and Clark, 2007).
[c] Ratio of soil organic carbon to 3 or 4 m depth in old Oxisols vs. in younger Oxisols; LS site (Table 6; Veldkamp et al., 2003).
[d] Range of ratios of maximum to minimum values from 18 0.5 ha plots in each of 12 successive years; LS site (Clark et al., 2013).
[e] Ratio between the 12-year maximum and 12-year minimum of yearly means of 18 0.5 ha plots; LS site (Clark et al., 2013).

Table 2. LAI observations in lowland old-growth tropical forests; ht: height.

LAI	Method	Area (ha)	Region	Site code	Source of data	Method details
6.00	Direct harvests	500	C. Amer.	LS	Clark et al. (2008)	Floor to canopy top leaf harvests, 55 points across 500 ha
5.10	LAI-2000	500	C. Amer.	LS	Olivas et al. (2013)	At > 1 m ht at 55 direct-harvest sites
4.9–6.0	Hemisph. photos	500	C. Amer.	LS	Olivas et al. (2013)	At > 1 m ht, 55 harvest sites; WinSCANOPY output types
3.90	Hemisph. photos	500	C. Amer.	LS	Olivas et al. (2013)	At > 1 m ht, 55 direct-harvest sites; gap light analyzer
2.7–4.85	Hemisph. photos	9	C. Amer.	LS	Loescher et al. (2003)	At > 1 m ht; $N = 6$ in each of 18 plots; three wet–dry seasons
5.70	Direct harvests	0.04	Amazon	MAN-McW	McWilliam et al. (1993)	Harvested four 10 × 10 m contiguous sections of forest
4.45	Hemisph. photos	2	Amazon	AGP-01,02	Jiménez et al. (2014)	At 1 m ht; $N = 26\,\text{ha}^{-1}$, unknown number of visits; HemiView
4.25	Hemisph. photos	1	Amazon	ZAR-01	Jiménez et al. (2014)	At 1 m ht; $N = 26\,\text{ha}^{-1}$, unknown number of visits; HemiView
5.58	Hemisph. photos	1	Amazon	MAN-K34	Marthews et al. (2012)	At 1 m ht; no details ("unpubl., S. Patiño")
5.25	Hemisph. photos	2	Amazon	CAX-06	Marthews et al. (2012)	At 1 m ht; no details ("unpubl., S. Patiño")
5.30	Hemisph. photos	1	Amazon	CAX-CTL	Metcalfe et al.. (2010)	At 1 m ht, 25 points in 1 ha, one date; HemiView
4.3–5.7	LAI-2000	1	Amazon	CAX-CTL	Metcalfe et al.. (2010)	100 points, unknown height, five dates
5.03	LAI-2000	3.1	Amazon	TAP-KM67	Malhado et al. (2009)	Monthly over 1 year; range of monthly values 4.8–5.2
4.8–5.1	LAI-2000	1.5	Amazon	TAP-A1,A4	Aragão et al. (2005)	Two forests, three 0.25 ha plots each, 25 points per plot, at unknown ht

upper and lower bounds for this biome, the accuracy of this range is also unknowable. Given these uncertainties, it will be important to maintain the actual field data (e.g., diameter and taxonomy of all stems) in a publically accessible archive, so that users could apply alternative allometries or estimation methods in the future.

For testing models against field observations of tropical-forest biomass (see Cleveland et al., 2015), a separate important issue is the within-forest spatial heterogeneity of EAB. For example, within a 10 ha area of French Guianan forest where EAB averaged 301 $\text{Mg}\,\text{ha}^{-1}$ (NOU-GP in Table 3) the range of the estimates for individual hectares was 230–416 $\text{Mg}\,\text{ha}^{-1}$ (Chave et al., 2001). A similarly large range among individual hectares was also found within the 50 ha plot on Barro Colorado Island, Panama (180–440 $\text{Mg}\,\text{ha}^{-1}$; Chave et al., 2003). Due to this local-scale variation, landscape-scale biomass observations would be required for most types of model–data fusion (except in the case of individual-based and forest demographic models (e.g., Hurtt et al., 2004), which explicitly incorporate this spatial heterogeneity).

Many models, particularly those that simulate forest demographics, use allometric equations to relate stem diameter to biomass. They also typically use estimated production of woody biomass to calculate diameter increments. In such cases, comparisons of both biomass and diameter increment for the same forest are therefore only sensible if the same allometric scaling is used. Again, detailed knowledge both of the data products (including EAB) and of model structures is critical.

Current ILAMB benchmarks for tropical regions include maps of aboveground biomass across the biome based on remote sensing products (e.g., Saatchi et al., 2011; Baccini et al., 2012). Large divergences between these maps (Mitchard et al., 2014) highlight the unresolved uncertainties due to method issues for both the remotely sensed data and the field observations (e.g., un-validated allometries, landscape-scale samples vs. a single 1 ha plot).

4.2.2 Coarse woody debris (CWD)

Estimates of tropical-forest CWD span a wide range and are method-dependent (see Table 4). The different methods in current use can produce significantly different estimates for the same site and time (e.g., the two 2005 estimates for JH-CLAY, Table 4). The spatial heterogeneity of standing and fallen CWD within tropical forests calls for landscape-scale sampling. CWD stocks are also likely to significantly change through time due to the temporal variation in tree mortality in this biome (see below).

4.2.3 Fine roots

Highly replicated, landscape-scale field observations of this C stock are potentially useful as a lower bound. Fine-root biomass is notoriously heterogeneous on multiple spatial scales. Studies within diverse tropical forests have demon-

Table 3. Landscape-scale estimates of aboveground biomass in lowland old-growth tropical forests. Estimates are based on diameters of all live stems in 9–72 ha per site. Lianas (+ or −): lianas included in biomass estimate?

EAB (Mg ha^{-1})	Measured area (ha)	Total study area (ha)	Region	Site code	Citation	Min. diam. (cm)	Lianas	Allometry used	Year(s)
242	12	12	Guianas	NOU-PP	Chave et al. (2001)	10	−	Brown (1997) (trop. wet)	1992
317	12	12	Guianas	NOU-PP	Chave et al. (2001)	10	−	Chave et al. (2001)	1992
428	12	12	Guianas	NOU-PP	Chave et al. (2001)	10	−	Lescure et al. (1983)	1992
376	12	12	Guianas	NOU-PP	Chave et al. (2008b)	10	−	Chave et al. (2005)	1992
381	12	12	Guianas	NOU-PP	Chave et al. (2008b)	10	+	Varied with plant type	1992
398	12	12	Guianas	NOU-PP	Chave et al. (2008b)	10	−	Chave et al. (2005)	2000–2002
403	12	12	Guianas	NOU-PP	Chave et al. (2008b)	10	+	Varied with plant type	2000–2002
301	10	10	Guianas	NOU-GP	Chave et al. (2001)	10	−	Chave et al. (2001)	1992–1994
356	10	10	Guianas	NOU-GP	Chave et al. (2008b)	10	−	Chave et al. (2005)	1992–1994
366	10	10	Guianas	NOU-GP	Chave et al. (2008b)	10	+	Varied with plant type	1992–1994
356	10	10	Guianas	NOU-GP	Chave et al. (2008b)	10	−	Chave et al. (2005)	2000–2002
366	10	10	Guianas	NOU-GP	Chave et al. (2008b)	10	+	Varied with plant type	2000–2002
281	50	50	C. Amer.	BCI	Chave et al. (2003)	1	+	Varied with plant type	1985–2000
307	50	50	C. Amer.	BCI	Chave et al. (2008a)	1	−	Chave et al. (2005)	1985–2005
161	9	500	C. Amer.	LS	Clark and Clark (2000)	10	−	Brown (1997) (trop. wet)	1997
321	72	6400	Amazon	DUC	de Castilho et al. (2010)	1	−	Higuchi et al. (1998)	2000–2003
324	72	6400	Amazon	DUC	de Castilho et al. (2010)	1	−	Higuchi et al. (1998)	2003–2005
380	20	100 000	Amazon	BDFFP	Pyle et al. (2008)	10	−	Chave et al. (2005)	1997–2004
334	20	100 000	Amazon	BDFFP	Pyle et al. (2008)	10	−	Chambers et al. (2001)	1997–2004
281	20	> 20	Amazon	TAP-KM67	Vieira et al. (2004)	35	−	Chambers et al. (2001)	1999
298	20	> 20	Amazon	TAP-KM67	Pyle et al. (2008)	35	−	Chambers et al. (2001)	1999–2005
394	20	> 20	Amazon	TAP-KM67	Pyle et al. (2008)	35	−	Chave et al. (2005)	1999–2005
272	25	25	Amazon	YASUNI	Valencia et al. (2009)	10	−	Chave et al. (2005)	1995–1999
282	25	25	Amazon	YASUNI	Chave et al. (2008a)	1	−	Chave et al. (2005)	1995–2000
274	25	25	Amazon	YASUNI	Valencia et al. (2009)	10	−	Chave et al. (2005)	2002–2003
190	10	10	Amazon	RIO-BR	Vieira et al. (2004)	35	−	Chambers et al. (2001)	1999
497	52	52	Asia	LAMBIR	Chave et al. (2008a)	1	−	Chave et al. (2005)	1992–2003
358	25	25	Asia	SINHA	Chave et al. (2008a)	1	−	Chave et al. (2005)	1993–1998
340	50	50	Asia	PASOH	Chave et al. (2008a)	1	−	Chave et al. (2005)	1986–2000
290	25	25	Asia	PALANAN	Chave et al. (2008a)	1	−	Chave et al. (2005)	1999–2003

Table 4. Landscape-scale estimates of coarse woody debris in lowland old-growth tropical forests. Standing dead: + indicates that it was included in the CWD estimate. When CWD was reported as Mg C, biomass was assumed to be 50 % C.

CWD (Mg ha^{-1})	Standing dead	Measured area (ha)	Total study area (ha)	Region	Site code	Min. diam. (cm)	Method used	Year(s)	Citation
32	+	20[a]	100 000	C. Amer.	BDFFP	10	Inventory + line intercept	1997–1999	Pyle et al. (2008)
96	+	20[c]	20	Amazon	TAP-KM67	2	Inventory + line intercept	2001	Rice et al. (2004)
50	+	12[d]	400	Amazon	JURU	10	Inventory + line intercept	2003–2004	Palace et al. (2007)
46	−	ca. 0.06[b]	12	Amazon	JH-SAND	10	Line intercept (610 m)	2005	Chao et al. (2008)
41	+	0.5	0.5	Amazon	JH-SAND	10	Stand-level inventory	2005	Chao et al. (2008)
31	−	ca. 0.06[b]	12	Amazon	JH-CLAY	10	Line intercept (640 m)	2005	Chao et al. (2008)
20	+	1	1	Amazon	JH-CLAY	10	Stand-level inventory	2005	Chao et al. (2008)
53	+	9	500	C. Amer.	LS	10	Stand-level inventory	1997	Clark et al. (2002)

[a] Indicates a 20 ha inventory for standing dead stems; line intercept used in subplots totalling 0.8 ha for fallen pieces > 10 cm diameter.
[b] Measured area estimated as 1 m × total length of transects.
[c] Indicates a 20 ha inventory for standing dead stems; subplot line intercepts (3.8 ha) for fallen pieces > 30 cm diameter; smaller areas for smaller pieces.
[d] Indicates a 12 ha inventory for standing dead stems; line intercept (12 km transect) for fallen pieces > 10 cm diameter; smaller areas for smaller pieces.

strated within-forest decreases in fine-root biomass with increasing microsite-scale availability of nutrients or water, as occurs along catenas or among the intercalated soil types in these forests (Palmiotto et al., 2004; Powers et al., 2005; Epron et al., 2006; Espeleta and Clark, 2007; Kochsiek et al., 2013; Noguchi et al., 2014; Wurzburger and Wright, 2015). Also, landscape-scale fine-root stocks can vary markedly through time. For example, fine-root stocks varied by 2.5 Mg ha^{-1} over a 7-year period in a Costa Rican wet forest (LS in Table 5; Espeleta and Clark, 2007). Dynamic ecosystem models would ideally hope to capture such time series.

Table 5. Estimates of fine-root stocks based on multiple hectares within each lowland old-growth tropical forest. Dead roots: + indicates that dead roots are included. When mass was reported as Mg C, C content was assumed to be 50 %.

Fine roots ($\mathrm{Mg\,ha^{-1}}$)	Total core area, $\mathrm{m^2}$	Total study area, ha	Region	Site code	Max. dia. (mm)	Soil depth (cm)	Dead roots	N, cores	Year(s)	Citation
5.9	?	?	Caribb.	BISLEY	20	0–10	–	?	2007	Cusack et al. (2011)
0.5	0.4	> 10	Amazon	TAP-SIL (clay)	2	0–10	–	144	7/99–5/01	Silver et al. (2005)
0.5	0.4	> 10	Amazon	TAP-SIL (sand)	2	0–10	–	144	7/99–5/01	Silver et al. (2005)
2.5[a], 3.5[a]	?	2	Amazon	TAP-DROU	2	0–10	+	20, 20	1998–1999	Nepstad et al. (2002)
3.4[a], 4.2[a]	?	2	Amazon	TAP-DROU	2	0–600	+	20, 20	1998–1999	Nepstad et al. (2002)
12.9[b]	0.36	ca. 30	Amazon	MAN-NOG	? (> 2)	0–40	+	9	? (pre-2014)	Noguchi et al. (2014)
2.4	0.03	> 10	C. Amer.	LS	2	0–40	+	15	9–10/2001	Powers et al. (2005)
1.1[c]	1.59	500	C. Amer.	LS (YO)	2	0–50	–	900[c]	10/1997–4/2004	Espeleta and Clark (2007)
1.6[c]	1.59	500	C. Amer.	LS (OO)	2	0–50	–	900[c]	10/1997–4/2004	Espeleta and Clark (2007)
5.0	0.03	> 10	Amazon	CC	2	0–40	+	15	10/2001	Powers et al. (2005)
2.8	0.03	> 10	C. Amer.	BCI	2	0–40	+	15	9–10/2001	Powers et al. (2005)
8.0	0.03	> 10	Amazon	KM41	2	0–40	+	15	11/2001	Powers et al. (2005)
5.6	0.07	4	Asia	MAEKL	3	0–30	–	3	11/1998	Takahashi et al. (2012)
4.5	0.06	52	Asia	LAMBIR	2	0–10	–	88	? (pre-2013)	Kochsiek et al. (2013)

[a] Two 1 ha plots, 20 cores in each, to 6 m depth.
[b] Dead roots = ca. 13 % of fine-root mass; fine-root mass in $\mathrm{Mg\,ha^{-1}}$ (three cores each): 8.7 (plateau), 10.5 (mid-slope), 19.8 (bottom).
[c] Six cores each in six 0.5 ha plots on younger Oxisol (YO) terraces and six 0.5 ha plots on older Oxisol (OO) plateaus; 25 dates.

As illustrated in Table 5, the methods used to quantify fine roots vary in multiple ways, including the maximum diameter of evaluated roots, the depth of soil cores, and whether or not dead roots are included. These method variations make cross-site comparisons and model benchmarking difficult.

A separate critical issue affects observations of fine-root stocks in all forest types, boreal to tropical: fine-root sampling in forests is usually restricted to the surface soils. No study has quantified fine roots all the way down the soil column in any tropical forest (see Table 5). The soils underlying these forests are often many meters deep. Nepstad et al. (1994) found live roots down to at least ca. 18 m depth under one Brazilian tropical forest (TAP-DROU in Table 5); over the depth interval 2–6 m, fine-root density was relatively constant but much reduced compared to that of surface fine roots. Given the great soil volume at depth, the contribution of deep fine roots both to total fine-root stocks and for ecosystem function may be significant in tropical forests. Models increasingly predict root stocks at different levels in the soil based on an assumed exponential decay down the vertical profile. In such cases model–data comparisons should be made for the actual soil layer of the measurements. Because all models require total root mass, however, extrapolation will be required in one domain or the other.

4.2.4 Coarse roots

There are as yet no stand-level observations of coarse roots in any forest type. In tropical forests, the field sampling for these spatially variable organs has been confined to harvesting the root systems of selected individual trees (e.g., Niiyama et al., 2010) or to sampling coarse roots in pits or trenches away from trees, thus missing their tap roots and other large roots (e.g., Castellanos et al., 1991; Veldkamp et al., 2003). A recent survey of the available harvest data (Waring and Powers, 2017) found that root : shoot ratios for individual trees from old-growth tropical forests averaged ca. 0.65, indicating the importance of this biomass component. Notably, this ratio strongly contrasts with the 0.21 multiplier commonly used to extrapolate tropical-forest coarse-root biomass from estimated aboveground live biomass (e.g., Malhi et al., 2009; Girardin et al., 2010; Quinto-Mosquera and Moreno, 2017).

4.2.5 Soil organic carbon (SOC)

SOC is strongly underestimated in all forest types (boreal to tropical) because it is rarely if ever quantified to depth (Jobbagy and Jackson, 2000). The limited tropical data in hand for subsurface SOC indicate that total SOC can dominate the C inventory in lowland tropical forests, where soils are commonly several to many meters deep (Sombroek et al., 2000). In two tropical forests where SOC was quantified to at least 3–4 m depth (Table 6), the cumulative SOC stock to the maximum sampled depth was roughly 10 times that at the surface (0–10 cm). Notably, cumulative SOC also exceeded the estimated C in aboveground live biomass (Table 6). Only in one of these cases (LS-younger Oxisol) was SOC quantified down to the parent material. In the other two, the sampling ended many meters shy of the total soil depth, thus missing large amounts of SOC. At the Amazonian site PARAGOM, where Trumbore et al. (1995) sampled SOC down to 8 m (Table 6), the soil shafts of Nepstad et al. (1994) actually extended down to 18 m depth.

The incompletely quantified SOC is a particularly critical data gap for tropical forests. There is accumulating evidence that the huge C stocks in the deep soils underlying many of these forests are not inert (e.g., Trumbore et

Table 6. SOC estimates based on sampling to > 1 m depth in multiple hectares in old-growth tropical forests. For each site, estimates are for cumulative SOC over depth range. EAB: estimated aboveground biomass.

Cumulative SOC $\mathrm{Mg\,C\,ha^{-1}}$	EAB $\mathrm{Mg\,C\,ha^{-1}}$	Total study area (ha)	Region	Site code	Soil depth (cm)	N, cores	Year	Citation
26	180[a]	> 10	Amazon	PARAGOM	0–10	24	1992	Trumbore et al. (1995)
102	180[a]	> 10	Amazon	PARAGOM	0–100	3	1992	Trumbore et al. (1995)
168	180[a]	> 10	Amazon	PARAGOM	0–300	3	1992	Trumbore et al. (1995)
206	180[a]	> 10	Amazon	PARAGOM	0–500	3	1992	Trumbore et al. (1995)
257	180[a]	> 10	Amazon	PARAGOM	0–800	3	1992	Trumbore et al. (1995)
29	83[b]	> 50	C. Amer.	LS-younger Oxisol	0–10	3	1999	Veldkamp et al. (2003)
123	83[b]	> 50	C. Amer.	LS-younger Oxisol	0–100	3	1999	Veldkamp et al. (2003)
213	83[b]	> 50	C. Amer.	LS-younger Oxisol	0–300	3	1999	Veldkamp et al. (2003)
35	74[b]	> 100	C. Amer.	LS-older Oxisol	0–10	3	1999	Veldkamp et al. (2003)
201	74[b]	> 100	C. Amer.	LS-older Oxisol	0–100	3	1999	Veldkamp et al. (2003)
330	74[b]	> 100	C. Amer.	LS-older Oxisol	0–300	3	1999	Veldkamp et al. (2003)
373	74[b]	> 100	C. Amer.	LS-older Oxisol	0–400	3	1999	Veldkamp et al. (2003)

[a] From Nepstad et al. (1994).
[b] From Clark and Clark (2000).

al., 1995; Veldkamp et al., 2003). At the Costa Rican LS site (Table 6), the SOC at 2–3 m depth was found to be strongly temperature-responsive (Schwendenmann and Veldkamp, 2006), indicating a vulnerability of this large tropical-forest C stock to future warming. Deep SOC (1–4 m depth) at this forest site was also found to mobilize with forest-to-pasture conversion (e.g., 30 $\mathrm{Mg\,C\,ha^{-1}}$ lost from this subsurface soil layer in ca. 30 years; Veldkamp et al., 2003). Changes in tropical-forest SOC, particularly in the deeper soil layers, could strongly impact the total forest C stocks and net C balance of this biome.

A second issue in tropical forests is that SOC shows marked spatial variation on all scales: from one square meter to the next (Powers, 2006) and across the major edaphic changes (topography, soil types; see Richter and Babbar, 1991) within a forest. An example of this within-forest heterogeneity is the significant difference in cumulative SOC content between two major soil types at the LS site (Table 6). Distributed and replicated sampling is therefore required to quantify this important C stock.

4.3 Ecosystem C fluxes

4.3.1 Net ecosystem CO_2 exchange (NEE)

> The eddy flux method has been criticized for uncertainty in its nighttime measurements. This is especially obvious in tropical areas, where nighttime turbulence is not well developed. Nevertheless, … Convincing results can be obtained from daytime eddy flux measurements… (Tan et al., 2013)

> It is clear that the choice whether or not to filter and replace nighttime [Amazon forest eddy flux] data represents the single major uncertainty in the whole estimation process. The choice can turn a very large carbon sink into a moderate one or even into a small source. (Araújo et al., 2002)

When taken at short time steps during the daytime, above-canopy measurements of the net ecosystem exchange (NEE) of CO_2 based on the eddy flux (also eddy covariance) technique have provided valuable indications of the environmental responses of tropical-forest physiology (e.g., depression of daytime NEE at high temperatures and/or high VPD; Doughty and Goulden, 2008; Vourlitis et al., 2011). No other technique provides direct field observations of the short-term climatic responses of forest-level CO_2 exchange. Further, when daytime eddy flux data from multiple years are filtered in a standard way (e.g., for periods of high light for estimating optimum uptake, as by Tan et al., 2013), they can indicate how or whether these environmental responses have varied through time.

For NEE at longer time steps (days to years), however, estimates based on the eddy flux technique in tropical forests do not provide reference-level field benchmarks for the models. Multiple issues for this technique in these forests create large uncertainties about the magnitude and even the sign of such estimates. The prevalence of still air conditions at night (e.g., 70–80 % of 30 min nighttime periods; Loescher et al., 2003: Costa Rica; Miller et al., 2004: Brazilian Amazon) means that the technique is inoperative or likely to be strongly biased during most nighttime periods. Studies have shown that the terrain irregularities typical of tropical forests can produce artifacts due to CO_2 movement into or out of an eddy flux site through lateral advection in these still air periods (Goulden et al., 2006; de Araújo et al., 2008; Tóta et al., 2008). In multiple studies (Araújo et al., 2002; Saleska et al., 2003; Miller et al., 2004) the eddy flux estimate of yearly NEE from a given year's worth of data switched from C source to C sink with different data filtering for these periods of slow air movement. Further uncertainty in eddy flux estimates of tropical-forest annual NEE is caused by the substantial data gaps due to heavy rainfalls, to frequent problems with instruments and with power, and to equipment damage from animals, treefalls, and lightning. For one forest eddy flux study in Borneo, the actual NEE data after data-filtering covered only 30 % of the 17-month study period (Katayama et al., 2013). Diverse methods are then used to fill the many periods of missing data (e.g., predicting daytime NEE based on radiation data, Katayama et al., 2013, or assuming a constant value for nighttime NEE, Loescher et al., 2003).

4.3.2 Gross primary productivity (GPP)

> … there is no way of directly measuring the photosynthesis or daytime respiration of a whole ecosystem of interacting organisms; instead, these fluxes are generally inferred from measurements of net ecosystem–atmosphere CO_2 exchange (NEE), in a way that is based on assumed ecosystem-scale responses to the environment. … Our [$^{13}C/^{12}C$] analysis indicates that daytime ecosystem respiration differed fundamentally from standard predictions that were based on nighttime NEE and temperature… (Wehr et al., 2016)

As underlined in the quote above, no method exists for directly observing total forest-level photosynthesis (also termed GPP). The existing field estimates of tropical-forest GPP have been derived based on modeling, assumed physiology, extrapolation, and/or incomplete field observations. Benchmark-level direct field observations are therefore lacking for this critically important C flux.

Although GPP estimates have been produced by tropical-forest eddy covariance studies, the sole CO_2 flux that is actually assessed with this technique is NEE, the small difference between two much larger, opposing fluxes (GPP and R_{eco}). As discussed above, eddy flux NEE data from tropical-forests are themselves highly uncertain and incomplete. The standard current approach for partitioning NEE into GPP and R_{eco} is based on assumptions about forest ecophysiology that have recently been challenged by findings from parallel ^{13}C / ^{12}C measurements in a temperate forest (Wehr et al., 2016).

Alternatively, bottom-up biometric approaches have been used to estimate GPP for some tropical-forest sites (e.g., Doughty et al., 2014; Malhi et al., 2015). These studies, carried out in a single 1 ha plot per forest, have been based on combining sparse direct observations of some components of production and respiration with intuitive estimates for, or omission of, many unmeasured components (see Sect. 2 and Table 7). In tropical forests, the summed C in the unmeasured processes may equal a significant fraction of total GPP (Clark et al., 2001a; Litton and Giardina, 2008).

4.3.3 Ecosystem respiration (R_{eco})

Similarly, existing eddy flux estimates for whole-forest respiration in this biome remain questionable due to multiple issues: (1) the uncertainty of the NEE estimate from which R_{eco} is inferred (see above), (2) the likelihood of lost (and/or extra) respiration due to lateral advection of CO_2 during the predominantly still nights (Goulden et al., 2006; Tóta et al., 2008), and (3) unresolved questions about the assumptions underlying the estimation of daytime R_{eco} from NEE (Chambers et al., 2004; Wehr et al., 2016; Wohlfart and Galvagno, 2017).

4.3.4 Autotrophic respiration (R_a) and heterotrophic respiration (R_h)

Benchmark-level field observations of these two fractions of R_{eco} are as yet lacking for tropical forests. Neither of these fluxes can be directly assessed in the field at the ecosystem level. Some estimates of stand-level R_a (e.g., Doughty et al., 2015, and included references) have been derived for different tropical forests in the Global Ecosystem Monitoring (GEM) project. These estimates were based on sparse field measurements in a single hectare of the studied forest of a subset of R_a components (fine-root respiration (estimated as soil CO_2 efflux minus that with root exclusion), canopy-leaf dark respiration, and tree-bole CO_2 efflux). These measurements were then combined with intuitive estimates for two unmeasured R_a components (daytime leaf respiration, respiration by coarse roots). The substantial CO_2 efflux from small-diameter wood (< 10 cm diameter) was not considered; however, in a Costa Rican forest this R_a component was estimated to account for 70 % of total woody CO_2 efflux, based on extensive sampling from mobile climb-up towers (Cavaleri et al., 2006). In the soil, the intimate interrelations among roots, root exudates, root symbionts, and soil microbes make the distinction between R_h and R_a both conceptually and methodologically challenging (Trumbore, 2006). An aspect of R_h that is rarely measured in tropical forests is the CO_2 efflux from decomposing coarse woody debris. This respiration component has been estimated at 6–16 % of total tropical-forest R_{eco}, based either on extrapolating spot field measurements of respiration from CWD to the stand level (Chambers et al., 2004: Central Brazilian Amazon) or on combining landscape-scale estimates of CWD stocks with inferred CWD turnover time (Hutyra et al., 2008: Eastern Brazilian Amazon; Cavaleri et al., 2008: Costa Rica).

4.3.5 Total net primary productivity (total NPP)

No benchmark field observations are available for total NPP. As is the case in all other forest types (Clark et al., 2001a), the field studies in tropical forests have been restricted to a

Table 7. The biometric components of total NPP in tropical forests (Mg C ha^{-1} yr^{-1}). Observed ranges (bold) are from examples in this paper and in Clark et al. (2001b). Guesstimates (italics) are for components as yet unquantified in tropical forests.

Component	Observed range	Guesstimate	Comment
VOC (volatile organic compound) production		*0.1–> 0.9*	Likely increase in isoprene prod. with warming
Aboveground wood production (larger stems)	**1.0–3.8**		Unverified estimates via off-site allometries
Wood prod. by smaller stems + hemiepiphytes		*≤ 0.1–0.38*	Rarely if ever quantified
Branch-shedding by live trees		*0.1–3.0*	Requires distinguishing pieces from dead trees
Twig litterfall (twigs ≤ 1 cm in diam.)	**0.4–1.3**		Likely underestimate (pre-collection decomp.)
Leaf litterfall	**2.9–3.4**		The surrogate for actual leaf production
Leaf mass lost to herbivory		*0.6–1.1*	Increasing with rising [CO$_2$] and C : N, C : P?
Leaf mass lost to decomposition, leaching		*0.1–1.0*	Signif. pre-collection losses in tropical forests
Reproductive litterfall	**0.2–0.7**		
Reproductive losses to consumers		*≥ 0.1–0.8*	Fruits are animal-dispersed, made to be eaten
Reproduction lost to pre-collection decomposition		*0.1–0.3*	
New nonstructural CHOs (stores)		*?*	
Coarse-root production		*0.2–2.3*	
Surface-soil fine-root production (0–30 cm)	**0.3–0.9**		
Deeper fine-root production (0.3 m to depth)		*0.1–0.5*	
Fine-root losses to herbivory & decomp.		*≫ 0*	As yet unstudied; possibly nontrivial
C exports to root symbionts (mycorrhizae, nodules)		*≫ 0*	A signif. NPP fraction in most tropical forests?
Root exudates		*≫ 0*	A large NPP fraction? Rising with [CO$_2$]?

subset of NPP components (Table 7). Those that remain unquantified could sum to a substantial fraction of total NPP (see also Clark et al., 2001a, b; Litton and Giardina, 2008; Cleveland et al., 2015). For the models, the sum of the NPP components assessed in the field provides a lower bound for total NPP.

Two NPP constituents missing from the field studies (Litton and Giardina, 2008) and from most models (Fatichi et al., 2014) so far are the amounts of new fixed C being lost (exported) from the plants belowground, either to root symbionts (nodules and/or mycorrhizae) or to the soil through root exudation. Isotopic evidence from a CO$_2$ enrichment study in a temperate forest indicated the likelihood of significant C export from the roots; belowground transfer of a substantial fraction of the assimilated C was found, with strong signals in mycorrhizal sporocarps and in soil respiration (a mix of R_h and R_a) but not in the fine roots (Steinmann et al., 2004). Most tropical trees support mycorrhizae (Janos, 1980), and legumes, potential N-fixers, are present in most tropical forests. The possibility therefore exists of considerable allocation of NPP to symbionts. This aspect of C cycling is practically unstudied in the biome. In one exceptional study in a Costa Rican forest (Lovelock et al., 2004), extra-radical hyphal production by arbuscular mycorrhizae at 0–10 cm soil depth was estimated at 1.5–1.9 Mg ha^{-1} yr^{-1}. Because the total plant-assimilated C going into new mycorrhizal fungal tissues also includes that incorporated into spores and sporocarps, the hyphae inside roots, and all the hyphae in the soil below 10 cm depth, this NPP component appears to be significant in this forest. Root exudation, as yet unstudied, is another potentially nontrivial portion of tropical-forest NPP. Another NPP constituent omitted from field C cycle studies is the production of volatile organic compounds (VOCs). Guenther et al. (1995) found total annual VOC emissions from tropical forests (isoprene, monoterpenes, other reactive VOCs, and other VOCs combined) to reach 75 g C m^{-2}, but with uncertainties greater than a factor of 3. Because production of isoprene by tropical trees and lianas strongly increases at higher temperatures (Keller and Lerdau, 1999), tropical warming is likely to increase this NPP constituent.

Opportunities for data–model fusion will be maximized by developing the C cycle models to explicitly specify those NPP components that have been assessed in the field. As recently reported by Negrón-Juárez et al. (2015), only three of the 10 ESMs in CMIP5 report "leaf NPP", "wood NPP", and "root NPP". The different production components are functionally distinct. In a landscape-scale field study at the Costa Rican LS site, the several field-quantified NPP components varied independently through 12 years, showing distinct relationships to the interannual variation in temperature, rainfall, and VPD (Clark et al., 2013). Below, we individually consider those biometric NPP components that have been assessed to date in tropical lowland forests.

4.3.6 Fine litterfall

In tropical forests, biometric aboveground NPP is typically dominated by short-lived tissues (Clark et al., 2001b). These are assayed as shed "fine litterfall" collected in litter traps (Table 8). Fine litterfall varies spatially within

Table 8. Landscape-scale estimates of the components of fine litterfall (leaf, reproductive, twig) in lowland old-growth tropical forests. Grd. traps: + or − indicate whether ground-level traps were used to collect large items (e.g., 3 m palm leaves); if not, leaf litterfall is likely to be underestimated.

Fine litterfall ($\mathrm{Mg\,ha^{-1}\,yr^{-1}}$)			Twig diam.	Trap area	Study area	Grd.				
Leaf	Reprod.	Twig	(cm)	($\mathrm{m^2}$)	(ha)	traps	Region	Site code	Citation	Years
5.7	0.7	1.4	?	60	50	−	Guianas	PISTE-ST.E	Puig and Delobelle (1988)	1978–1981
5.8	0.7	1.8	< 1	30	10	−	Guianas	NOU-PP	Chave et al. (2008b)	2001–2007
6.6	0.8	2.5	< 1	50	12	−	Guianas	NOU-GP	Chave et al. (2008b)	2001–2007
6.8	1.3	0.9	< 1	81	500	+	C. Amer.	LS	Clark et al. (2013)	1997–2009
6.4	0.6	1.4	?	17	ca. 10	−	C. Amer.	BCI	Leigh et al. (1990)	1972–1979

each tropical forest. When assessed in 18 0.5 ha plots distributed within one neotropical forest (**LS**, Table 8), the plots differed (max − min) in annual leaf litterfall by 3.8 to 6.3 $\mathrm{Mg\,ha^{-1}\,yr^{-1}}$, depending on the year; for reproductive litterfall, the across-plot range was > 2 $\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ in most of the 12 years (data in Table S2 in Clark et al., 2013). Landscape-scale data are therefore needed for reference-level benchmarks for this aspect of tropical-forest C cycling. Because the three components of fine litterfall are functionally distinct, they are considered individually below.

4.3.7 Leaf litterfall (vs. leaf production)

In field studies of biometric NPP (termed NPP*; Clark et al., 2001a), leaf litterfall over a given study interval is typically taken as a surrogate for leaf production over that interval. Stand-level leaf production itself has not been quantified in the field in tropical forests. In most tropical forests, leaf litterfall is the largest contributor to aboveground NPP* (Clark et al., 2013, and included references). It can be a misleading surrogate for leaf production in terms of both mass and timing. One method issue is the difficulty of quantifying the very large fallen leaves in tropical forests (e.g., 3 m long palm leaves). Ground-level and/or very large traps are required to collect these large items of fine litter (Villela and Proctor, 1999) but are rarely used. In addition, in tropical forests leaf litterfall undervalues leaf production due to two types of pre-collection losses (Table 7; also see Clark et al., 2001b). One is the mass loss from pre-collection decomposition and leaching of the shed leaves in the hot, humid conditions. Some leaves hang up in the vegetation and decompose above the ground. When Frangi and Lugo (1985) suspended old leaves from palms in a Puerto Rican forest, they found that roughly half the leaf mass was lost through decomposition in 4 months. A second issue is the leaf mass removed by herbivores (Table 7). Partial leaf damage (holes in fallen leaves) was estimated at ca. 0.8 $\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ in a lowland Peruvian forest (Metcalfe et al., 2013); in addition, leaf-monitoring studies (Lowman, 1984; Filip et al., 1995) have shown that an equivalent amount or more may typically be lost to herbivores that remove entire leaves.

One potential approach for models would be to explicitly include the processes of herbivory and decomposition losses that occur between leaf production and leaf shedding, therefore facilitating a direct comparison. In lieu of this, model–data comparisons should take into account the low bias of leaf litterfall observations. In cases in which leaf litterfall is conflated with leaf production for the purposes of determining allocation to the leaf fraction, the resulting allocation underestimate might lead to underestimation of LAI.

A separate issue is that the seasonal timing of leaf production can differ from that of leaf litterfall, as found by Reich et al. (2004) in a Venezuelan tropical forest (in most species studied, although there was some degree of correlation). In many tropical forests, leaf litterfall typically peaks at the time of the yearly maximum soil dry-down (Wagner et al., 2016); this timing can be distinct from that of actual leaf production. Such a timing disjunct will complicate attempts to evaluate the seasonality of tropical-forest NPP and C allocation when leaf litterfall is used as the surrogate for production (e.g., Doughty et al., 2014).

4.3.8 Twig litterfall (vs. twig production)

Estimates of twig litterfall should be treated as a lower bound for twig production. In tropical forests, twig litterfall (Table 8) is likely to strongly underestimate actual production due to substantial mass loss before collection. In a New Guinea rain forest, when Edwards (1977) compared canopy-collected live twigs with a diameter < 1 to < 1 cm diameter twigs in the litter traps, the fallen twigs were found to have already lost 36–40 % of their mass, presumably due to decomposition and/or leaching when they were still attached to the branches above.

4.3.9 Reproductive litterfall (vs. reproductive production)

The biometric surrogate for reproductive production, reproductive litterfall (Table 8), is likely to undervalue production by at least 50 %. This NPP component is not easily quantified at the stand level. Tropical forests are typically dominated by animal-dispersed plants. The consumers are likely to remove most of the fruits produced, leaving the crumbs to fall into the litter traps. In a Puerto Rican palm forest, for example, fruit production assessed by direct observation over time exceeded the fruit mass in litter traps by a factor of 14 (Lugo and Frangi, 1993). Similarly, in a Colombian tropical forest, the estimate of fruit production based on observing from platforms and from climbing ropes was double the estimate based on fruit mass in the litter traps (Parrado-Rosselli et al., 2006).

For multiple reasons, this NPP component merits attention for the models. Many land surface models do not specifically include the carbon allocation to reproduction; this omission implies corresponding overestimates of stocks of other carbon pools (e.g., roots, stems, leaves). Demographic models, in contrast, typically do specify reproductive allocation, which is needed to drive forest recruitment (Moorcroft et al., 2001). Secondly, reproductive tissues are nutrient-rich (e.g., in nitrogen, phosphorus, and cations) and thus likely play a significant role in the cycling of those nutrients. Reproductive status could influence nutrient resorption and thus reallocation of carbon (Tully et al., 2013). A third issue is that this production component could be responding to climatic and/or [CO_2] changes. Two recent tropical-forest studies suggest multi-decadal increases in forest-level reproduction (reproductive litterfall, Clark et al., 2013; flowering incidence, Pau et al., 2013).

4.3.10 Aboveground wood production (EABI)

As for aboveground woody biomass (above), field estimates of aboveground wood production, also termed EABI (estimated aboveground biomass increment), are unverified and highly uncertain. This production component is based on measurements at two successive censuses of the diameters of all live stems in the study plot that exceed an arbitrary diameter limit (usually 10 cm); these data are then used for allometric estimation of the tree's aboveground biomass at both times. EABI is calculated as the sum of the estimated biomass increments of all the stems that survived the interval, plus the estimated increments above the specified size limit of the recruits, those smaller stems that grew past the minimum size by the second census (see Clark et al., 2001a). One method variant (Chave et al., 2008b; Pyle et al., 2008), equating the census-interval growth of new recruits to their total estimated mass at the second census, substantially overestimates these small trees' contribution to stand growth; before reaching the 10 cm diameter limit, most small trees in tropical forests have grown very slowly over decades (see Clark and Clark, 2001; Rozendaal et al., 2015).

As for estimates of aboveground biomass, because EABI depends on an unverified allometric relationship between stem diameter and stem biomass, all values of this metric involve unquantifiable uncertainty. When different allometries are applied to the same set of diameter data, different estimates of EABI can be produced (e.g., duplicate estimates at site TAP-KM67; Table 9). Determining which if any of such estimates are reasonable would require follow-up on-site verification of the underlying allometry (Clark and Kellner, 2012).

Given the heterogeneity of biomass dynamics within a tropical forest, data–model fusion exercises and site-level model testing call for landscape-scale field data for EABI. Individual-based or demographic models (e.g., ED, Moorcroft et al., 2001) that address the small-scale spatial heterogeneity within a forest landscape are the exceptions to this. In spite of this metric's unquantifiable uncertainty, when estimated on the landscape scale and in the same way over a long series of successive periods, repeated annual estimates can provide valuable guidance for the models with respect to both long-term trends in this productivity component and its climatic and [CO_2] responses. For example, 12-year records of EABI from the LS site revealed highly significant sensitivities of landscape-scale EABI to the inter-year changes in nighttime temperatures, VPD, and [CO_2] (Clark et al., 2013).

4.3.11 Fine-root production

Field estimates of fine-root production at the landscape level in tropical forests provide a useful lower bound for this NPP component. Due to the method challenges, fine-root production has not been well quantified in any forest type, boreal to tropical. In the tropical-forest biome, because of the notorious variation in fine-root stocks on all spatial scales (Espeleta and Clark, 2007; Powers et al., 2005), robust assessment of fine-root production for a given forest would require highly replicated and distributed sampling. Unfortunately, this production component has only rarely been assessed in multiple hectares of a tropical forest (Table 10). A second critical limitation is that the field measurements to date in this biome have been confined to the surface soil (0 to ≤ 30 cm depth). There are no field observations from tropical forests of production by the deeper fine roots (live fine roots were found to at least 18 m depth in one Amazon forest; Nepstad et al., 1994).

Variable methods for assessing fine-root production (different soil depths and root sizes, inclusion or exclusion of dead roots; Table 10) also make cross-site comparisons difficult. The usual approach in tropical forests, in-growth cores, is likely to strongly underestimate production due to lags before root in-growth and the likelihood of roots dying and decomposing before soil cores are retrieved; in a temperate pine forest, production estimates based on in-growth cores aver-

Table 9. Landscape-scale estimates of aboveground wood production (EABI, $\mathrm{Mg\,ha^{-1}\,yr^{-1}}$) in lowland old-growth tropical forests. Int. length: the length of the interval between censuses. Min. dia.: the minimum diameter of the measured stems in each census.

EABI	Plot area (ha)	Study area (ha)	Region	Site code	Citation	Min. dia. (cm)	Allometry used	Method for recruit growth	Int. length (yr)	Years
8.3[a]	20	?	Amazon	TAP-KM67	Pyle et al. (2008)	10	Chave et al. (2005)	Est. biomass[c]	2–4	1999–2005
7.2[a]	20	?	Amazon	TAP-KM67	Pyle et al. (2008)	10	Chambers et al. (2001)	Est. biomass[c]	2–4	1999–2005
6.6	20	100 000	Amazon	BDFFP	Pyle et al. (2008)	10	Chave et al. (2005)	Est. biomass[c]	5	1997–2004
5.7	20	100 000	Amazon	BDFFP	Pyle et al. (2008)	10	Chambers et al. (2001)	Est. biomass[c]	5	1997–2004
8.7	12	12	Guianas	NOU-GP	Chave et al. (2008b)	10	Chave et al. (2005)[b]	Est. biomass[c]	8	1992–2002
8.0	10	10	Guianas	NOU-PP	Chave et al. (2008b)	10	Chave et al. (2005)[b]	Est. biomass[c]	8	1992–2002
3.7	9	500	C. Amer.	LS	Clark et al. (2013)	10	Brown (1997)	Inc. > 10 cm[4]	1	1997–1998
5.0	9	500	C. Amer.	LS	Clark et al. (2013)	10	Brown (1997)	Inc. > 10 cm[4]	1	2005–2006
5.0	50	50	C. Amer.	BCI	Chave et al. (2008a)	1	Chave et al. (2005)	?	5	1985–2005
6.8	24	24	Amazon	YASUNI	Chave et al. (2008a)	1	Chave et al. (2005)	?	5	1995–2000
7.0	50	50	Asia	PASOH	Chave et al. (2008a)	1	Chave et al. (2005)	?	5	1986–2000
7.2	52	52	Asia	LAMBIR	Chave et al. (2008a)	1	Chave et al. (2005)	?	5	1992–2003
4.9	16	16	Asia	PALANAN	Chave et al. (2008a)	1	Chave et al. (2005)	?	4	1999–2003
7.4	25	25	Asia	SINJA	Chave et al. (2008a)	1	Chave et al. (2005)	?	5	1993–1998

[a] Stems with a 10–< 35 cm diameter measured in subplots totalling 4 ha; stems ≥ 35 cm diameter measured over 20 ha.
[b] The allometry of Chave et al. (2005) was used for trees; for lianas, the allometry Schnitzer et al. (2006) was used.
[c] The contribution to EABI from recruits is defined as their total estimated biomass.
[d] The contribution to EABI from recruits is defined as their estimated growth above 10 cm diameter.

Table 10. Estimates of fine-root production ($\mathrm{Mg\,ha^{-1}\,yr^{-1}}$) from multiple hectares within lowland old-growth tropical forests.

Fine-root prod.	Measured area ($\mathrm{m^2}$)	Study area (ha)	Region	Site code	Root diam. (mm)	Method	Depth (cm)	Time to retrieval (months)	Citation	Years
0.7	0.04	?[a]	C. Amer.	EARTH	< 2	In-growth cores	0–10	24	Alvarez-Clare et al. (2013)	2008–2010
3.5[b], 3.3[b]	0.28	2[b]	Asia	LAMBIR	< 10	In-growth cores	0–30	3	Kho et al. (2013)	2008–2009

[a] Data from the control plots of a fertilization experiment, one in each of four blocks separated by ≥ 50 m.
[b] Data from 1 ha in clay soil and 1 ha in sandy soil; cores extracted every 3 months over 1 year.

aged 54 % lower than those from minirhizotrons (Hendricks et al., 2006). Whether root herbivory removes a significant fraction of fine-root production (Lauenroth, 2000) is as yet unstudied in tropical forests.

4.4 Tree mortality

> … [in a steady-state landscape] about 98.0 to 99.7 % of forest land is in a carbon-sequestering stage; the remaining 0.3 to 2 % is emitting carbon … from natural breakdown (tree death, gap formation), disturbance (wind break, fire), … pest outbreak … Unless sensors capture such short-term "emission" events …, they will commonly signal net carbon uptake … Plot-based carbon flux measurements … cannot produce a realistic picture of a landscape's contribution to carbon sequestration. (Körner, 2003)

> … a more comprehensive sampling scheme that includes large-area data (e.g., large plots and remote sensing) and robustly characterizes disturbance size distribution is required to understand tropical forest dynamics and its impact on carbon balance. (Di Vittorio et al., 2014)

Biomass losses from tree mortality are a critical determinant of forest biomass stocks (McDowell et al., 2011). In tropical forests, strong spatiotemporal variation in these losses makes quantifying and tracking them highly challenging. Illustrating this variation are the contrasting losses from two 1 ha plots in a Borneo forest in each of three intervals (LAMBIR site; Kho et al., 2013; Table 11). Tropical-forest disturbance regimes predominantly involve frequent small-scale canopy gaps (< 150 $\mathrm{m^2}$) caused by branchfalls or treefalls; larger forest openings from storms, blowdowns, or extreme drought are increasingly rare in time and space as these disturbances increase in size (Chambers et al., 2013; Gloor et al., 2009; Magnabosco Marra et al., 2014; Marvin et al., 2014; di Vittorio et al., 2014). A study in the central Amazon combining remote sensing and ground observations (di Vittorio et al., 2014) found mortality losses to follow a power-law distribution with disturbed area, up to and including the region's extremely large blowdowns; these researchers concluded that the biomass losses observed solely in existing plots would be an inaccurate indicator (biased low) of landscape-scale dynamics. A separate compli-

Table 11. Estimated mortality-driven biomass loss ($\mathrm{Mg\,ha^{-1}\,yr^{-1}}$) from multiple-hectare samples in lowland old-growth tropical forests. Meas. area: plot area in which all stems were measured. Int. (yr): interval between censuses.

Mortality biomass loss	Meas. area (ha)	Study area (ha)	Region	Site code	Citation	Minimum stem diam. (cm)	Allometry used	Int. (yr)	Years
15[a], 1[a]	2[a]	52	Asia	LAMBIR	Kho et al. (2013)	10	Chave et al. (2005)	5	1992–1997
5[a], 15[a]	2[a]	52	Asia	LAMBIR	Kho et al. (2013)	10	Chave et al. (2005)	6	1997–2003
5[a], 2[a]	2[a]	52	Asia	LAMBIR	Kho et al. (2013)	10	Chave et al. (2005)	5	2003–2008
6.1	52	52	Asia	LAMBIR	Chave et al. (2008a)	1	Chave et al. (2005)	5	1992–2003
4.7	16	16	Asia	PALANAN	Chave et al. (2008a)	1	Chave et al. (2005)	4	1999–2003
8.4	25	25	Asia	SINJA	Chave et al. (2008a)	1	Chave et al. (2005)	5	1993–1998
5.4	50	50	Asia	PASOH	Chave et al. (2008a)	1	Chave et al. (2005)	4	1986–2000
5.3	50	50	C. Amer.	BCI	Chave et al. (2008a)	1	Chave et al. (2005)	5	1985–2005
6.2	24	24	Amazon	YASUNI	Chave et al. (2008a)	1	Chave et al. (2005)	5	1995–2000

[a] Data from 1 ha in clay soil and 1 ha in sandy loam soil within the 52 ha plot; from Fig. 2 in Kho et al. (2013).

cation is the disproportionate influence on biomass stocks from the deaths of scattered very large trees. In French Guianan old-growth forest (Rutishauser et al., 2010), such tree deaths were found to largely drive the heterogeneity in biomass dynamics among plots and through time. Unsurprisingly, given these sources of variation, Galbraith et al. (2013) found a 6-fold variation among wood turnover rates (23–129 years) calculated from small individual tropical-forest plots. Landscape-scale field observations are clearly required to guide the models with respect to tropical-forest mortality and its counterpart, biomass turnover. Parallel monitoring of larger forest expanses with remote sensing would further improve such estimates.

An observational finding important for the C cycle models is the strong temporal variation in tropical-forest tree mortality. Mortality spikes have been observed in both neotropical and Asian tropical forests in extreme climatic events such as the strong El Niños of 1982/83 and 1997/98 and the 2005 Amazon drought (Clark, 2004; Williamson et al., 2001; van Nieuwstadt and Sheil, 2005; Phillips et al., 2009).

Some models specify stochastic dynamics of tree death (Fyllas et al., 2014; Smith et al., 2014). Many models attempt to simulate the responses of tree mortality to changes in vegetation stress (McDowell et al., 2013; Powell et al., 2013) but more aggregated models typically use a simple turnover parameter (Galbraith et al., 2013, reviewed by McDowell et al., 2013). Introducing more robust mortality benchmarks based on combining structured ground data with satellite observations (e.g., Kellner and Hubbell, 2017) and also explicitly linking large mortality losses to extremes of climatic stressors (e.g., Phillips et al., 2009) should help modelers move towards a more process-based representation of tropical-forest mortality.

4.5 Directional trends and climatic and [$\mathrm{CO_2}$] responses of C cycling

A valuable class of benchmarks for the C cycle models will be landscape-scale field observations of the decadal changes in and climatic and $\mathrm{CO_2}$ responses of C stocks and fluxes in tropical forests. Given the complexities described above for quantifying forest C stocks and fluxes across time and space, detecting incremental changes caused by external drivers is a particularly difficult problem. Long series of landscape-scale measurements at annual or greater intervals are rare for this biome.

To illustrate this type of response benchmarks Table 12 lists the significant relationships revealed by a 12-year landscape-scale study of annual biometric aboveground NPP (ANPP*) in a Costa Rican forest (Clark et al., 2013). Through that period, one of the four biometric ANPP* components, EABI, showed highly significant negative impacts from two climatic stressors and a small positive response to increasing [$\mathrm{CO_2}$]. One other production component, reproductive litterfall, also showed a small positive association with [$\mathrm{CO_2}$]. Replicating such quantitative analyses across the biome and through the coming decades would greatly contribute to more accurate C cycle models for these forests. The long-term yearly C cycle studies that have now been implemented in many large tropical-forest plots of the CTFS network (Anderson-Teixeira et al., 2015) are a major step in that direction.

4.6 Local meteorology

Sparse and intermittent climatic monitoring in all tropical regions makes the interpolated global gridded climatic datasets unreliable for this biome (see Deblauwe et al., 2016). In addition, sub-daily meteorological records are critically needed for driving C cycle models. High-quality climatic records from tropical-forest field sites would be particularly important resources for model–data fusion exercises and merit in-

Table 12. Climatic and [CO_2] responses (±95 % confidence intervals) of C cycling in lowland old-growth tropical forests. EABI (estimated aboveground biomass increment) and reproductive litterfall are in units of $Mg\,ha^{-1}\,yr^{-1}$.

Aspect, C cycling	Response	*P*	N, years	Site code	Years	Citation
EABI	-0.95 ± 0.37 per °C increase in yearly mean of daily T_{min}	0.00015	12	LS	1997–2009	Clark et al. (2013)
EABI	-0.03 ± 0.01 per % incr. in hours of VPD > 1 kPa, dry season	0.00015	12	LS	1997–2009	Clark et al. (2013)
EABI	$+0.021 \pm 0.015$ per additional ppmv of annual [CO_2]	0.006	12	LS	1997–2009	Clark et al. (2013)
Reproduct. litterfall	$+0.012 \pm 0.011$ per additional ppmv of annual [CO_2]	0.01	12	LS	1997–2009	Clark et al. (2013)

Table 13. Local meteorological records for lowland old-growth tropical forests (one example site). Qa/Qc: +, documented quality control; Cons.: +, adjusted for internal consistency over total record; Gaps.: +, missing data for some periods. Location: sensors on a ground-level station (grnd) or above-canopy tower (ab-can).

Site code	Time step	Climatic metric	Location	Qa/ Qc	Gaps.	Cons.	Time period	Weblink or other data source
LS	Daily	Rainfall	grnd	+	+	+	1/1963–1992	www.ots.ac.cr/meteoro/default.php?pestacion=2
LS	Daily	Rainfall	grnd	+	−	+	9/1992–2016	www.ots.ac.cr/meteoro/default.php?pestacion=2
LS	Daily	Radiation (pyr)	grnd	+	+	−	3/1992–2016	www.ots.ac.cr/meteoro/default.php?pestacion=2
LS	Daily	Max T_{air}, min T_{air}	grnd	+	−	+	4/1982–2016	www.ots.ac.cr/meteoro/default.php?pestacion=2
LS	Daily	Mean T_{air}	grnd	+	−	+	3/1992–2016	www.ots.ac.cr/meteoro/default.php?pestacion=2
LS	30 min	Radiation (pyr, PAR)	grnd	+	+	−	3/1992–2016	On request to deborahanneclark@gmail.com
LS	Hourly	T_{air}, RH, rainfall	grnd	+	+	−	6/1992–2016	On request to deborahanneclark@gmail.com
LS	30 min	T_{air}, RH, rainfall	grnd	+	+	−	1/2003–2016	On request to deborahanneclark@gmail.com

clusion among the benchmark field observations of the ILAMB effort.

For a catalogue of such local climatic records, key accompanying information should include whether the data are from a ground-level met station or from above-canopy sensors, and whether the records have been screened, corrected to maintain internal consistency, and gap-filled. At the example site in Table 13, multiple adjustments to the records were required after the manual instruments were relocated and then augmented with an automated system (see Clark and Clark, 2011). The calculation ($[T_{max} + T_{min}]/2$) used in the early record to estimate daily T_{mean} from maximum and minimum thermometer data was found to significantly differ from the actual logged daily T_{mean} at this site. Splicing the prior estimated record to the current record of logged T_{mean} would have spuriously indicated an abrupt 1 °C cooling in the site's T_{mean} record (see Fig. 2 in Clark and Clark, 2011). The long-term record for T_{mean} was therefore confined to the automated data. The early records for rainfall and $T_{max/min}$ also required adjustment by cross-site and/or cross-sensor regression. Such issues likely affect many local met records from tropical-forest field sites. The longer records are likely to include periods both before and after the introduction of an automated station. At many sites, station siting is also likely to have changed over time.

5 Conclusions: next steps

A community-consensus catalogue of the benchmark-level field observations directly relevant to C cycling would be a major advance. As we found in this first effort for tropical forests, the development of such catalogues will require the active participation of both field researchers and modelers. Involvement of field researchers with extensive experience in C cycling studies in the target biome will be critical for identifying reference-level field data. Such an effort will require their firsthand expertise with field methods and conditions in the target ecosystems, along with a broad knowledge of the relevant literature. Field ecologists and modelers are now collaborating at the outset of field experiments to determine the necessary observations for testing ecosystem-level hypotheses embedded in the theoretical components of ESMs. This same interdisciplinary approach is important for identifying appropriate field observations for effective model–data fusion. Given the increasing use of models as tools for understanding ecosystem processes, a new generation of scientists who can work across empirical and theoretical fields will be key for this effort.

Data catalogues need to be "living" resources, constantly updated as new information comes in and as ecological insights and methods develop in each biome. For the ongoing updating, a web-based, moderated system would seem to be the strongest approach. With such a system, field researchers worldwide could actively participate, continuously offering

Table 14. Site codes and descriptors for the field sites in the benchmark data tables. MAP: mean annual precipitation; MAT: mean annual temperature.

Site code	Region	Study site	Citation	Elevation (m)	Lat.	Long.	MAP mm	Years of MAP data	MAT °C	Years of MAT data
AGP-01,02	Amazon	Amacayacu, Colombia	Jiménez et al. (2014)		3°43′ S	70°18′ W	3342	1973–2008	26	1973–2008
BDFFP	Amazon	N of Manaus, Brazil	Pyle et al. (2008)		2°30′ S	60° W	2285			
CC	Amazon	Cocha Cashu Stn., Peru	Powers et al. (2005)		11°54′ S	71°72′ W	2165	?–pre-2004		
CAX-06	Amazon	Caixuana, Brazil	Marthews et al. (2012)		−1.72917	−51.4736	2272			
CAX-CTL	Amazon	Caixuana, Brazil	Metcalfe et al. (2010)		−1.72917	−51.4736	2272			
DUC	Amazon	Reserva Ducke, Brazil	de Castilho et al. (2010)	40–140	2°55′ S	59°59′ W	ca. 2300	?–pre-2010	ca. 26	pre-2010
JH-CLAY	Amazon	Jenaro Herrera, Peru	Chao et al. (2008)		4°55′ S	73°44′ W	2500–2700	?–pre-2001	26–27	pre-2001
JH-SAND	Amazon	Jenaro Herrera, Peru	Chao et al. (2008)		4°55′ S	73°44′ W	2500–2700	?–pre-2001	26–27	pre-2001
JURU	Amazon	Juruena, Brazil	Palace et al. (2007)		10°49′ S	58°48′ W				
KM41	Amazon	KM41 reserve, Brazil	Powers et al. (2005)		2°30′ S	60°0′ W	2650	?–pre-2001		
MAN-NOG	Amazon	30 km N of Manaus, Brazil	Noguchi et al. (2014)		2°36′ S	60°8′ W				
MAN-K34	Amazon	Manaus K34 tower, Brazil	Marthews et al. (2012)				2285^a	1961–1990^a		
MAN-McW	Amazon	N of Manaus, Brazil	McWilliam et al. (1993)				2285^a	1961–1990^a		
RIO-BR	Amazon	Rio Branco, Acre, Brazil	Vieira et al. (2004)		10°07′ S	67°62′ W	1940^b	1969–1990^b		
PARAGOM	Amazon	Paragominas, Pará, Brazil	Trumbore et al. (1995)		2°59′ S	47°31′ W	1750	?–pre-1994		
TAP-A1,A4	Amazon	Tapajós, Pará, Brazil	Aragão et al. (2005)		2°51′ S	54°58′ W	1909^c	1967–1990^c		
TAP-DROU	Amazon	Tapajós, Brazil drought site	Nepstad et al. (2002)		2.9° S	54.95° W	2000	?–pre-2002		
TAP-KM67	Amazon	Tapajós, Brazil tower site	Pyle et al. (2008)		2°51′ S	54°58′ W	1909^c	1967–1990^c	25	pre-1995
TAP-SIL	Amazon	Tapajós, Brazil	Silver et al. (2005)		2°64′ S	54°59′ W	1909^c	1967–1990^c	25	pre-1995
YASUNI	Amazon	Yasuní, Ecuador	Valencia et al. (2009)	216–248	0°41′ S	76°24′ W	3100			
ZAR-01	Amazon	Zafire, Colombia	Jiménez et al. (2014)		4°0′ S	69°53′ W	3342	1973–2008	26	1973–2008
BCI	C. Amer.	Barro Colorado I., Panama	Chave et al. (2003)	120–160^d	9°15′ N^d	79°85′ W^d	2637	1929–2001		
LS	C. Amer.	La Selva, Costa Rica	Clark et al. (2013)	37–150	10°26′ N	83°59′ W	4537	1997–2009	25.1	1997–2009
EARTH	C. Amer.	EARTH Univ., Costa Rica	Alvarez-Clare et al. (2013)	30	10°11′ N	84°40′ W	3464	?–pre-2012	25.1	
PISTE-ST.E	Guianas	Piste Saint Elie, French Guiana	Puig and Delobelle (1988)	10–50	5° N	53° W	3238	1978–1981	26	1978–1981
NOU-GP	Guianas	Les Nouragues, French Guiana	Chave et al. (2001)	100 (−411)	4°50′ N	50°42′ W	2757	1989–1998		
NOU-PP	Guianas	Les Nouragues, French Guiana	Chave et al. (2001)	100 (−411)	4°50′ N	50°42′ W	2757	1989–1998		
BISLEY	Caribb.	Luquillo (Bisley), Puerto Rico	Cusack et al. (2011)	260	18°20′ N	65°48′ W	3500			
LAMBIR	Asia	Lambir, Sarawak, Borneo	Chave et al. (2008a)	124–209	4.1865	114.017	2921			
PALANAN	Asia	Palanan, Philippines	Chave et al. (2008a)	85–140	17.0402	122.388	2607			
PASOH	Asia	Pasoh, Malaysia	Chave et al. (2008a)	70–90	2.982	102.313	1973			
SINHA	Asia	Sinharaja, Sri Lanka	Chave et al. (2008a)	424–575	6.4023	80.4023	3379			
MAEKL	Asia	Mae Klong Stn., Thailand	Takahashi et al. (2012)	150–350	14°35′ N	98°52′ E	1650	pre-1995	ca. 25	pre-1995

[a] Rainfall data from Manaus, in Vieira et al. (2004).
[b] Rainfall data from Rio Branco, in Vieira et al. (2004).
[c] Rainfall data from Santarém, in Vieira et al. (2004).
[d] Elevation data from CTFS website; latitude and longitude from http://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=157.

new field observations for consideration and also correcting or augmenting current entries. Proposed updates, however, should be prescreened by a team of volunteer researchers and modelers with the relevant expertise.

We have identified here examples of reference-level field observations from lowland old-growth tropical forests. Now what is clearly needed is a much broadened discussion among the wider tropical research community, both to refine the benchmark criteria for these forests and to contribute observations on a continual basis going forward. A similar parallel effort is also greatly needed to identify data benchmarks for the highly distinct C cycling processes taking place in degraded and successional tropical forests, which may account for half or more of the forest area across the tropics (Chazdon, 2014). Yet a different set of benchmarks would be needed to characterize C cycling in tropical montane forests, an ecologically distinct class of tropical forests.

Our effort here provides a starting point for addressing the modeling community's need for reference-level field observations from the tropical-forest biome. As is evident from our review, the field data for our target forests are woefully sparse, and the uncertainties around the major C stocks and fluxes are large. The complete lack of information for some potentially important aspects of C cycling, such as root exudation and the C exports from plants to their symbionts, contributes to these uncertainties. More generally, there is a clear need for observations of all aspects of C cycling to be made on the landscape scale and through time, to quantify their dynamics and any directional trends. Such studies need to be made across an expanded set of forests that spans all major tropical regions. Long-term records of local meteorology at sub-daily resolution, another critical requirement for the models, are available for few study sites in this biome. Analyses of the climatic and CO_2 sensitivities of C cycling, which require long series of observations (more than a decade) at a study site, would be of great value for evaluating model results but remain rare. These identified needs provide a set of exciting and urgent priorities for the community of tropical field ecologists. At the same time, our review has provided numerous valuable points of reference from the field studies to date in tropical forests. Following the vision of the ILAMB effort, many aspects of the existing field observations can serve as benchmarks for developing and evaluating the land models with respect to the tropical-forest biome.

Data availability. No datasets were used in this article.

Author contributions. All authors collaborated in the writing of the paper.

Competing interests. The authors declare that they have no conflict of interest.

Acknowledgements. This work was made possible by the support of the US Geological Survey John Wesley Powell Center for Analysis and Synthesis. The support from the Powell Center included funding the participation of Shinichi Asao. Deborah A. Clark was supported by US National Science Foundation LTREB grants DEB-1147367 and DEB-1357112. Tana E. Wood was supported by US Department of Energy, Terrestrial Ecosystem Sciences grant DE-SC0011806 and by the USDA Forest Service International Institute for Tropical Forestry in collaboration with the University of Puerto Rico. Xiaojuan Yang was supported by the Next-Generation Ecosystem Experiments-Tropics and the Biogeochemistry–Climate Feedbacks Scientific Focus Area (BGC Feedbacks SFA) of the US Department of Energy, Office of Science, Office of Biological and Environmental Research. Peter B. Reich was supported by the US Department of Energy, Office of Science (DE-SC0012677). Sasha Reed was financially supported by US Department of Energy, Terrestrial Ecosystem Sciences grant DE-SC0011806 and by the US Geological Survey Ecosystems Mission Area. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. David B. Clark constructively commented on the paper.

Edited by: Anja Rammig
Reviewed by: two anonymous referees

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