Review and synthesis

Review of allometric equations for major land covers in SE Asia: Uncertainty and implications for above- and below-ground carbon estimates

Jia Qi Yuen [a], Tak Fung [b], Alan D. Ziegler [a,*]

[a] Department of Geography, National University of Singapore, Singapore
[b] Department of Biological Sciences, National University of Singapore, Singapore

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ABSTRACT

Our review of biomass studies conducted for 11 Southeast Asian countries, Papua New Guinea, and southern China uncovered 402 above-ground and 138 below-ground biomass allometric equations for the following major land covers: forest, peat swamp forest, mangrove forest, logged over forest, orchard and tree plantation, rubber plantation, oil palm plantation, bamboo, swidden fallow, and grassland/pasture/shrub land. No equations existed for non-swidden agroforest and permanent croplands, two other important land covers involved in current and projected land-cover transitions. We also found 245 stem-volume equations and 50 height-diameter equations. Applying existing allometric equations out of convenience is potentially a key source of uncertainty in above- and below-ground carbon stock estimates in many SE Asian landscapes. Differences in environmental conditions and vegetation characteristics should preclude the use of many pre-existing equations at locations outside of the geographical location where they were developed, without first verifying their applicability. While use of site-specific equations is preferred to reduce uncertainty in estimates, there are few in existence for many land covers and many geographical areas of the region. For example, few or no equations exist for Brunei, Cambodia, Laos, Papua New Guinea, Singapore, and Timor Leste. Ten or fewer above-ground biomass equations exist for rubber plantation, oil palm plantation, non-swidden agroforest, grassland/pasture/shrublands, and permanent croplands for the entire region. Even site-specific equations can introduce uncertainties to biomass estimates if they were determined from an insufficient sample size. Difficulties associated with sampling below-ground root biomass accurately often leads to allometric equations that potentially under-estimate below-ground biomass. In addition, substantial errors may be present if these below-ground equations are conveniently used by researchers in lieu of site-specific measurements. Although the importance of including wood density in allometry is increasingly recognized, only 26 of the reviewed studies did so. Ideally, when wood density values are used to estimate biomass, new on-site measurements should be taken, rather than relying on pre-existing values. This review demonstrates that more research in SE Asia is needed on biomass in general, specifically for several land covers including peat swamp forest, rubber and oil palm plantations, bamboo, swidden fallow, non-swidden agroforest, and permanent cropland. Importantly, for the purpose of informing the development and implementation of policies and programs such as REDD+, our meta-analysis highlights the pressing need to address the insufficient number of allometric equations and the possible inappropriate use of some when estimating vegetation biomass related to current and potential land cover changes in the region.

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Contents

* Corresponding author at: Block AS02-03-01, 1 Arts Link Kent Ridge, Singapore 107568, Singapore.
  E-mail address: geoadz@nus.edu.sg (A.D. Ziegler).

1. Introduction

Vegetation biomass is the living organic matter that is produced by photosynthesis (Brown, 1997). Biomass can be partitioned into two components: (1) above-ground biomass, which includes the stems and any branches, leaves, flowers, and fruits above the soil surface; and (2) below-ground biomass, which is often divided for convenience into the root crowns, coarse roots (>2 mm diameter), and fine roots (<2 mm diameter) (eg., Kny, 1894; Vadeboncoeur et al., 2007; Zani and Suratman, 2011). The division of a plant into the stems, branches, leaves, flowers, fruits and roots is an established concept in botany (e.g., Nuttall, 1841; Harvard, 1884). Quantifying vegetation biomass is necessary for evaluating biological and economic productivity, fuel accumulation, and nutrient allocation. Recently, biomass measurements have become crucial for determination of carbon sequestration in vegetation and for understanding the impacts of land-cover changes on carbon fluxes (Cole and Ewel, 2006; Heryati et al., 2011b; Addo-Fordjour and Rahmad, 2013). Carbon biomass is either determined directly from harvested samples through analytical means, for example, with a carbon–nitrogen analyzer, or calculated as a fraction of measured biomass—on the order of 0.37–0.53 for various types of plants and trees (Yuen et al., 2013).

The advent of carbon accounting schemes such as REDD+ (Reducing Emissions from Deforestation and Forest Degradation and Enhancing Carbon Stocks) has created widespread interest in determining carbon biomass in vegetation in tropical areas (http://www.un-redd.org/aboutredd). REDD+ was put forth by the United Nations Framework Convention on Climate Change (UNFCCC) Conference of Parties (COP) as a means to reduce carbon dioxide emissions to the atmosphere by giving developing countries financial incentives to conserve (and increase) carbon stocks within their forests (Mertz et al., 2012). To qualify for REDD+ payouts, countries must typically monitor carbon biomass stock in the land covers in question accurately over time (Hein and van der Meer, 2012; Murdiyarso et al., 2012).

The most precise method for determining carbon biomass is to destructively harvest all plants, partition each by mass into various constituent components (e.g. stem, branches, leaves, flowers, fruits, roots) and subsequently determine the C content of the various components analytically. However, uprooting vegetation, especially trees, is time consuming, costly, and sometimes illegal. With respect to the latter, cutting forest trees often goes against the goal of conserving forests (Basuki et al., 2009; Djomo et al., 2010; Jachowski et al., 2013). An alternative approach is to use established allometric equations to estimate biomass and then calculate carbon biomass as a fraction of this value.

Allometry in the context of tree biomass estimation refers to mathematical equations relating biomass of an entire tree or individual tree components (e.g., stems, branches, leaves or roots) to one or more easily measured biophysical factors, such as tree diameter at breast height, tree height, or wood density (Kira and Shidei, 1967; Whittaker and Woodwell, 1968; Baskerville, 1972; Banaticla et al., 2007; Basuki et al., 2009; Kuyah et al., 2012). Main stem volume equations can also be developed from these variables (cf. Whittaker and Woodwell, 1968; Kusmana et al., 1992; Hiratsuka et al., 2005; Heryati et al., 2011b; Khun et al., 2008), with stem biomass calculated by multiplying stem volume with wood density (Brown and Lugo, 1984; Nogueira et al., 2007; Somogyi et al., 2007). In this case, biomass expansion factors are then applied to estimate biomass of branches and leaves (cf. Brown, 1997). Through allometric equations, above- and below-ground biomass in large stands can be estimated without the need to cut trees (Kira and Shidei, 1967; Kenzo et al., 2009). The obvious paradox here is that the equations must be based on destructive sampling of vegetation somewhere before they can be applied generally (Basuki et al., 2009; Chave et al., 2014).

Previously, we surmised that one important source of uncertainty in above-ground and below-ground carbon stock estimates for several land covers in Southeast Asia was the application of pre-existing allometric equations in locations differing from where they were determined (Ziegler et al., 2012; Yuen et al., 2013). In the prior works we did not report details regarding the sources of error related to the use of allometric equations in biomass assessments. Herein, we extend those analyses by reviewing studies reporting above- and below-ground allometric equations with the intention of (a) providing a summary of country-by-country allometric equations for the various land covers associated with major land use transitions in SE Asia; (b) discussing the limitations and uncertainties associated with the use of pre-existing allometric equations; and (c) identifying further directions for allometry research. The review is part of a larger effort to assess the effects of ongoing and projected land cover conversion on carbon stocks in the region (Fox et al., 2012, 2014; Ziegler et al., 2012; Yuen et al., 2013; Webb et al., 2014).

2. Background

In biology, allometry was conceived as the study of how properties of an organism change with size-related traits (Huxley, 1932). These relationships were found to be commonly described by power-laws of the form $Y = aX^b$, where Y and X are the related variables, a is the normalization constant (Sileshi, 2014), and b is the exponent. Thus, the power-law has been referred to as a law of simple allometry (Huxley and Teissier, 1936). In fact, power-law relationships in biology were recognized by Galton (1879) about half a century before publication of Huxley's book (Huxley, 1932). Based on evidence that a number of biological properties scale allometrically with body size according to a power-law over many orders of magnitude, the metabolic theory of ecology has been propounded in the last few decades (Brown et al., 2004). Within forestry, the power-law is one of the most common forms for allometric equations used to calculate biomass (Chan et al., 2013; Banaticla et al., 2007). If the errors for a sample of trees are assumed to be additive, then a simple biomass equation has the following form:

$$B_i = aX_i^b + \varepsilon_i \tag{1}$$

where B_i is either above-ground or below-ground biomass of the ith tree sampled, or the biomass of a component of this tree (Mg); X_i is the value of a trait for the ith tree sampled, for example the diameter at breast height (DBH_i, cm) or height (H_i, m); and ε_i is the error term for the ith tree sampled. However, when (1) is fitted to empirical data, the error often increases with biomass, resulting in heteroscedasticity. Thus, errors are usually assumed to be multiplicative, giving

$$B_i = aX_i^b \varepsilon_i \tag{2}$$

Following log transformation, this equation can be represented as:

$$\log B_i = \log a + b \log X_i + \log \varepsilon_i \tag{3}$$

which can be fitted using ordinary least squares (OLS) regression to give estimates of a and b, denoted by $\hat{a}$ and $\hat{b}$, respectively. If the errors ($\log \varepsilon_i$) are uncorrelated and exhibit homoscedasticity, then $\hat{a}$ and $\hat{b}$ are unbiased estimates with the lowest variance (best linear unbiased estimates, or BLUEs). Normality of the residuals is not required to perform the regression, but it is required to construct exact confidence and prediction intervals for a and b. Normality of residuals also implies that $\log B_i$ follows a normal distribution, such that B_i follows a lognormal distribution. Let the mean and variance of $\log B_i$ be denoted by μ and σ^2 respectively; the mean of B_i is then given by $\exp[\mu + (\sigma^2/2)]$ (McAlister, 1879). This formula shows that obtaining the mean biomass on the untransformed scale is not simply a case of exponentiating μ, which corresponds rather to the (smaller) median biomass (McAlister, 1879). Thus, the mean of B_i is often estimated by $\exp(\bar{x})$ multiplied by the correction factor

$$C_F = \exp\left(\frac{s^2}{2}\right) \tag{4}$$

where $\bar{x}$ and s^2 are the sample mean and variance on the transformed scale that are used to estimate μ and σ^2, respectively (Baskerville, 1972; Chave et al., 2005; Dietz and Kuyah, 2011). However, $\exp(\bar{x})C_F$ is not an unbiased estimate of the mean of B_i (Finney, 1941). Rather, the unbiased estimate takes the form of an infinite series with increasing powers of $1/n$, where n is the sample size (Finney, 1941):

$$\exp(\bar{x})\exp\left[\frac{s^2}{2}\left(1 - \frac{s^2(s^2+2)}{4n} + \frac{s^4(3s^4+44s^2+84)}{96n^2} + \cdots\right)\right] \tag{5}$$

From expression (5), we see that C_F can lead to a positive bias in biomass estimates. Indeed, biomass overestimates have been found after application of C_F, suggesting positive biases (Madgwick and Satoo, 1975; Hepp and Brister, 1982).

Although OLS regression provides a rigorous method of estimating parameters of a power-law model, it is not the only method of estimation available. Other methods include maximum likelihood and Bayesian techniques (Sileshi, 2014). In particular, heteroscedasticity in the error terms in Eq. (1) can be accounted for without using multiplicative errors and a log-transformation by modeling the errors as following a normal distribution with a variance that is an increasing function of X_i, for example as an exponential function of X_i (Parresol, 1999). The resulting equation can then be fitted to the data using generalized least squares (GLS), which allow BLUEs and construction of both confidence and prediction intervals (Parresol, 1999). This method of accounting for heteroscedasticity may be preferable because there is no need to transform the parameter estimates found. Interestingly, application of one method could result in estimates that lie outside the confidence or credible intervals of other methods (Sileshi, 2014). Thus, application of more than one method may be the best approach. However, an analysis of estimates from five methods applied to six tree datasets resulted in substantial overlap of intervals (Sileshi, 2014), suggesting substantial redundancy of methods.

Returning to biomass equations, the basic power-law form in Eqs. (1) and (2) has been extended to other forms that allow for inclusion of a wider range of biological complexity. For example, instead of using X_i to represent the value of just one trait, it can represent a function of trait values, such as D_iH_i and $D_i^2H_i$. In particular, this extension allows inclusion of wood density ρ_i (kg/m³), for example as in the following equation (Chave et al., 2014):

$$B_i = a\left(\rho_i H_i D_i^2\right)^b \varepsilon_i \tag{6}$$

Other extended forms include quadratic and exponential equations, as shown respectively in the following examples (Brown, 1997):

$$B_i = a + bD_i + cD_i^2 + \varepsilon_i \tag{7}$$

$$B_i = e^{a + b\log D_i + c(\log D_i)^2} \varepsilon_i \tag{8}$$

where a, b and c are model constants. The latter exponential equation with just the first two terms in the exponent summation is equivalent to a power-law equation. Another common extended form of allometric relationship incorporates root:shoot ratios, which describe relationships between above- and below-ground biomass (Yuen et al., 2013).

The extended allometric Eqs. (7) and (8) can be fitted to data using the same techniques that can be applied to power-law equations (discussed above). When presented with a set of nested model equations, choice of which one to use can be decided using selection procedures based on likelihood-ratio tests, such as stepwise forward selection and backward elimination. However, these procedures have been criticized because dependence of successive tests render problematic the determination of the significance level according to which variables are eliminated—and in any case, the final threshold chosen is arbitrary (Burnham and Anderson, 2002). Thus, procedures based on minimizing information criteria, such as AIC and BIC (Akaike, 1973, 1978a,b; Schwarz, 1978; Burnham and Anderson, 2002), have been proposed, which reflect a trade-off between the bias and variance in a model. However, minimizing these criteria only allows identification of the best model out of a particular set considered. Thus, it is important to specify a set of candidate models that are mathematically and biologically defensible. To account for uncertainty in model selection due to the use of a finite sample of data,

techniques have been developed that average results from a set of models that could potentially be selected when considering many samples (Burnham and Anderson, 2002).

Despite the extra flexibility afforded by the extended allometric Eqs. (7) and (8), there are caveats associated with their use. One is that inclusion of more variables increases the potential for multi-colinearity, especially when the variables are functions of the same trait, as in Eq. (7), or when the value of one variable is estimated from that of another. The presence of multicolinearity violates an assumption of OLS regression and can change the magnitudes and signs of parameter estimates, as well as greatly inflate estimates of their variance and the width of prediction intervals (Sileshi, 2014). Therefore, it is advisable to remove variables causing multicolinearity by calculating the variance inflation factor or using partial least squares regression (Sileshi, 2014).

Another caveat is that the inclusion of extra terms may have little or no biological meaning. In this case, the model may give a good description of the particular dataset to which it is fit, but could poorly represent the data generating process, thereby resulting in poor general predictive ability (Sileshi, 2014). Thus, selecting a model from a candidate set with all combinations of specified variables and equation forms ("data dredging") is strongly discouraged (Burnham and Anderson, 2002; Sileshi, 2014). In addition, the predictive ability of a fitted model should be tested, for example, through cross-validation (Sileshi, 2014).

An interesting debate involves developing the most accurate allometric equation for a particular data set versus developing one that holds for a strict interpretation of "allometry", as well as sound model development practices using independent prediction variables (cf. Sileshi, 2014; Picard et al., 2015). This debate also relates to the development of pantropical equations (e.g., Chave et al., 2014). Picard et al. (2015) found that inclusion of height as a separate predictor in addition to DBH significantly improved fits to observed biomasses. Likewise, Feldpausch et al. (2012) showed that including height significantly improved the fit of tropical above-ground biomass. Biologically, inclusion of height is reasonable because trees with the same DBH often have different stem tapering relationships (Nogueira et al., 2008; Temesgen et al., 2015). Kohyama et al. (2003) found that understorey species in a Bornean mixed dipterocarp forest had shorter heights at the same trunk diameter, and deeper crowns at the same tree height, than canopy species because of morphological adaptation by understorey species to deep shade. Height, and potentially crown size, are therefore useful variables for accounting for specific differences in plant architecture or phenotypic plasticity that may be related to the growing conditions in particular locations (Callaway et al., 1994; Archibald and Bond, 2003; Goodman et al., 2014; Kohyama et al., 2003). Further, in the development of pantropical equations, based on analyses of data from 58 sites worldwide and involving >4000 trees, Chave et al. (2014) concluded that a generic tree diameter–height relationship can be used because the relationship is linearly related to bioclimatic stress, which is a function of temperature variability, precipitation variability, and drought intensity. Thus, Picard et al. (2015) disagree with the implication of Sileshi (2014) that variables used in allometric models should be selected a priori and based on theoretical scaling relationships between (typically two) biological variables (i.e., a strict sense of allometry).

Allometric equations may be species-specific, developed from sampling a particular plant species, usually at a particular location. On the other hand, multi-species equations have been developed for heterogeneous land covers, often forests, which are composed of so many different species that it is not feasible to sample all. For example, up to 300 species per hectare may be found in some diverse tropical forests (de Oliveira and Mori, 1999). In such cases, allometric models are typically developed from a handful of the most dominant species. In the Bago Mountains of Myanmar, for example, Chan et al. (2013) found that an equation developed using only the six most dominant species (55 out of 160 sample trees) yielded above-ground biomass values that were not greatly different from a multi-species equation determined from 53 species (mean above-ground biomass of 17.22 vs 18.15 kg). In some instances, vegetation age is incorporated to produce age-specific equations (either for single or multiple species).

Often, there is a need to estimate the total above-ground or below-ground biomass of a tree with the measured biomass and trait values of various components of the tree. For example, information is typically provided on three main components of a tree above the ground: the wood of the main axis (bole), the bole bark and the crown (consisting of branches and foliage) (Parresol, 1999). For each component, an equation relating biomass to various measurable traits can be derived using the methods mentioned above. To obtain an equation for the total biomass, it is necessary to ensure that this equation gives values that are equal to the sum of the values from the component equations – i.e., additivity (Kozak, 1970). At first this problem may seem trivial because the component equations can be summed to produce an equation for total tree biomass. Indeed, if the component biomasses are independent and are linear functions of the same set of traits (e.g., are all specified by Eq. (7)), then the equation for total biomass can be derived by simply summing the component equations, and the corresponding confidence and prediction intervals can be derived (Kozak, 1970; Chiyenda, 1983; Chiyenda and Kozak, 1984). However, complexities arise because (i) the component equations may be functions of different sets of traits; (ii) the component biomasses are likely to be estimated from the same set of data on the same tree, so that the error terms are actually correlated (Parresol, 1999); and (iii) the component equations can be intrinsically non-linear.

In the case where the component biomass equations are linear but are functions of different sets of traits, the total biomass equation can be derived by estimating the parameters for each component equation using constrained OLS regression, with the constraint being that coefficients of irrelevant traits are set to zero, and then summing the equations (Chiyenda, 1983; Chiyenda and Kozak, 1984). To account for dependence among component equations as well (errors in different equations are correlated), a technique called seemingly unrelated regression (SUR) can be used (Zellner, 1962; Cunia and Briggs, 1984, 1985). This technique works by estimating the variance–covariance structure of the errors using OLS, and then estimating the remaining parameters by using GLS to minimize the sum of squared residuals produced by both the component equations and total equation (set equal to sum of component equations to ensure additivity). In the case where the component equations are non-linear, a non-linear version of SUR (NSUR) called non-linear joint GLS can be used (Gallant, 1987; Parresol, 1999, 2001). NSUR can incorporate non-linear component equations that are separate functions of different sets of traits, as well as dependence of errors among equations. Incorporation of correlated errors has the effect of reducing variance of parameter estimates and the widths of confidence and prediction intervals, as was demonstrated by application of NSUR to slash pine trees (*Pinus elliottii*) in plantations in the U.S. (Parresol, 2001) and Pyrenean oak trees (*Quercus pyrenaica* Willd.) in Portugal (Carvalho and Parresol, 2003).

While allometric equations are usually used to estimate tree biomass, they can also be developed for any other vegetation type within a land cover, dominant or non-dominant. Lianas, for example, may make up as much as 38% of species diversity and contribute up to 30% of the total above-ground biomass within some tropical forests (Addo-Fordjour et al., 2008; Schnitzer and Bongers, 2011). Therefore, biomass estimates in forest ecosystems,

especially disturbed ones, will be under-estimated if these plants are ignored. Equations for estimating above-ground liana biomass can be found in the works of Addo-Fourdjour and Rahmad (2013), Feng et al. (1998), Lü et al. (2010) and Schnitzer et al. (2006). Allometric equations have also been developed for stranglers (Culmsee et al., 2010) and young shoots (Yoneda et al., 1999). While we acknowledge the availability of allometric equations for these types of secondary vegetation forms, our review will focus on the primary forms that comprise major land covers in SE Asia.

3. Methods

We focus on 12 major land covers related to important land cover and land-use transitions now taking place in SE Asia, including Papua New Guinea (PNG) and Southern China (Xishuangbanna and Hainan Island): forest (FOR), peat swamp forest (PF), mangrove (MAN), logged over forest (LOF), orchard and tree plantation (OTP), rubber plantation (RP), oil palm plantation (OP), bamboo (BAM), swidden fallow of any length (SF), non-swidden agroforest (AGF), grassland, pasture and shrub land (GPS) and permanent cropland (PC) (Yuen et al., 2013). Thus, the review provides information for Brunei, Cambodia, Indonesia, Lao PDR, Malaysia, Myanmar, Philippines, PNG, Singapore, Southern China (Xishuangbanna and Hainan Island), Thailand, Timor Leste and Vietnam.

For each land cover, we compiled literature-reported allometric equations for calculating total biomass, above-ground and below-ground (root) biomass. The literature search was done using Google, Google Scholar, Scopus and individual journal databases using various permutations of the following keywords: above-ground, below-ground, roots, root:shoot ratio, allometry, allometric equations, carbon, biomass, Southeast Asia, tropics, mangrove, forest, peat swamp forest, orchard and tree plantation, logged forest, secondary forest, rubber plantation, oil palm plantation, bamboo, swidden fallow, shifting cultivation, slash and burn, agroforest, grassland, permanent cropland and agriculture. The individual country names were also used as search keywords. In addition, bibliographies were used to find relevant articles. Relevant non-English articles (e.g. Chinese, Japanese, Malay and Thai) were included if found. By doing so, we identify gaps in equation coverage and assess limitations in equation development (Henry et al., 2013). Allometric equation databases exist for other geographical regions, including North and Latin America (cf. Ter-Mikaelian and Korzukhin, 1997; Jenkins et al., 2003; Návar, 2009), Europe

(cf. Zianis et al., 2005), Africa (cf. Henry et al., 2011) and Australia (cf. Eamus et al., 2000; Keith et al., 2000). Allometry in SE Asia is represented in the GlobAllomeTree database (cf. Henry et al., 2013) – however, the countries covered include only Cambodia (five unique biomass equations, 35 unique volume equations), Indonesia (five unique biomass equations) and Vietnam (73 unique biomass equations, 8 unique volume equations). We incorporated all these biomass and volume equations from the GlobAllomeTree database into our compilation. While the number of equations may seem sizeable, they come from a handful of studies (Cambodia: United States Agency for International Development, 1962; FAO, 1998; Forestry Administration, 2004; Khun et al., 2008; Kiyono et al., 2011), Indonesia (Kiyono et al., 2011) and Vietnam (Dung et al., 2012; Hung et al., 2012a,b,c; Huy et al., 2012; Phuong et al., 2012b). The status of this database is discussed below in Section 5.

We report four categories of equations: (1) multi-species equations; (2) age-specific/multi-species equations; (3) species-specific equations; and (4) age-specific/single-species equations. Species-specific equations were grouped under the dominant land cover in which the data used to derive the equations were collected. The reported allometric equations were mostly either species-specific or multi-species equations.

We also include equations for tree height and stem volume in the synthesis. Reported equations include those that estimate total above- or below-ground biomass as well as separate equations for estimating each tree component (e.g., stem, branches, leaves, flowers and fruits). To facilitate future use of the compiled equations, we compiled information on species and plant components, author-reported regression statistics, number of trees harvested, locations of field sites, diameter ranges for which the equations are valid, and other relevant bibliographic information (Table S1 for above-ground biomass; Table S2 for below-ground biomass; Table S3 for volume equations and Table S4 for height equations). Metadata for these equations are summarized in Tables 1–3 in the main text.

Owing to limited data and lack of standardization of botanic nomenclature (cf. Maxwell, 2004), a variety of vegetation types were lumped into common land-cover classes. For example, forest combined both evergreen and deciduous lowland forest types. Ambiguous forest types were also placed in this class. The orchard and tree plantation group included a range of timber and fruit-bearing trees, including *Acacia*, *Eucalyptus*, *Tectona* (teak) and cocoa. Owing to limited data, all types of swidden fallow were

Table 1
Comparison of number of project-specific above-ground biomass allometric equations for twelve types of land-cover in 11 Southeast Asian countries, Papua New Guinea, and Southern China.

Country/class[a]	FOR	PF	MAN	LOF	OTP	RP	OP	BAM	SF	AGF	GPS	PC	Total
Brunei													0
Cambodia	8			1									9
Indonesia	18	14	19	22	76	2	3	1	8				163
Lao PDR					2			2	1				5
Malaysia	5	1	4	3	10	2	3	5	10				43
Myanmar			1		3			7	1		1		13
Papua New Guinea	1				2								3
Philippines			3		23			4					30
Singapore													0
Southern China	10		2	11		4			8				35
Thailand	11		12		25			4					52
Timor Leste													0
Vietnam	17		7	3	4			7			2		40
Tropics[b]	12		1										13
Total	82	15	49	40	145	8	6	30	28	0	3	0	

[a] The twelve types of land cover considered are: forest (FOR), peat swamp forest (PF), mangrove (MAN), logged-over forest (LOF), orchard and tree plantation (OTP), rubber plantation (RP), oil palm plantation (OP), bamboo (BAM), swidden fallow of any length (SF), non-swidden agroforest (AGF), grassland, pasture and shrub land (GPS) and permanent cropland (PC).
[b] Equations do not belong to a specific country, and many were compiled with data collected worldwide.

Table 2
Comparison of number of project-specific root/below-ground biomass allometric equations for twelve types of land-cover in 11 Southeast Asian countries, Papua New Guinea and Southern China.

Country/class[a]	FOR	PF	MAN	LOF	OTP	RP	OP	BAM	SF	AGF	GPS	PC	Total
Brunei													0
Cambodia	2			1									3
Indonesia	1	2	7	2	44								56
Lao PDR					2				1				3
Malaysia	1	1	3		6		1		5				17
Myanmar			1										1
Papua New Guinea					1								1
Philippines					2								2
Singapore													0
Southern China	9		2	11		2			8				32
Thailand	1		5		14								20
Timor Leste													0
Vietnam			1										1
Tropics[b]	2												2
Total	16	3	19	14	69	2	1	0	14	0	0	0	

[a] The twelve types of land cover considered are: forest (FOR), peat swamp forest (PF), mangrove (MAN), logged-over forest (LOF), orchard and tree plantation (OTP), rubber plantation (RP), oil palm plantation (OP), bamboo (BAM), swidden fallow of any length (SF), non-swidden agroforest (AGF), grassland, pasture and shrub land (GPS) and permanent cropland (PC).
[b] Equations do not belong to a specific country, and many were compiled with data collected worldwide.

Table 3
Number of (1) multi-species, (2) age-specific/multi-species, (3) species-specific and (4) age-specific/single-species allometric equations available for calculating above- and below-ground biomass in 10 major types of land cover in SE Asia, Papua New Guinea and Southern China.

	FOR	PF	MAN	LOF	OTP	RP	OP	BAM	SF	GPS
Aboveground										
Total no. of equations	82	15	45[a]	40	145	8	6	30	28	3
No. of multi-species equations	61 (74%)	9 (60%)	7 (16%)	17 (43%)	8 (6%)	0	0	3 (10%)	4 (14%)	1 (33%)
No. of age-specific/multi-species equations	0	0	1 (2%)	7 (18%)	1 (1%)	0	0	0	7 (25%)	0
No. of species-specific equations	21 (26%)	6 (40%)	33 (73%)	12 (30%)	71 (49%)	4 (50%)	4 (67%)	23 (77%)	4 (14%)	2 (67%)
No. of age-specific/single-species equations	0	0	4 (9%)	4 (10%)	65 (45%)	4 (50%)	2 (33%)	4 (13%)	13 (46%)	0
Belowground										
Total no. of equations	16	3	19	14	69	2	1	0	14	0
No. of multi-species equations	11 (69%)	3 (100%)	6 (32%)	4 (29%)	2 (3%)	0	0		1 (7%)	
No. of age-specific/multi-species equations	0	0	1 (5%)	4 (29%)	0	0	0		6 (43%)	
No. of species-specific equations	5 (31%)	0	10 (53%)	6 (43%)	29 (42%)	1 (50%)	0		0 (0%)	
No. of age-specific/single-species equations	0	0	2 (11%)	0	38 (55%)	1 (50%)	1 (100%)		7 (50%)	

The land covers considered are: forest (FOR), peat swamp forest (PF), mangrove (MAN), logged-over forest (LOF), orchard and tree plantation (OTP), rubber plantation (RP), oil palm plantation (OP), bamboo (BAM), swidden fallow of any length (SF), and grassland, pasture and shrub land (GPS). Numbers in parentheses represent the percentage distributions.
[a] Figure is less than that in Table 1 because four equations were developed from sampling in more than one country – Thailand and Indonesia – and were counted for both countries in Table 1. Here, they were not counted twice (cf. Poungparn et al., 2003; Komiyama et al., 2005; Table S1).

combined. Peat and mangrove forests were separated from other forest types because they are a unique wetland ecosystem with large stores of terrestrial carbon and are highly threatened by on-going conversions (Page et al., 2006; Murdiyarso et al., 2010). The logged-over forest category included various types of regenerating, secondary and artificial forests. Unless authors provided indication of prior swiddening, all disturbed non-plantation forests were put in this category. While bamboo is common on fallow lands, and is a grass, we placed it in a separate group because of its unique morphology and high potential for carbon sequestration (Lobovikov et al., 2012).

4. Results

4.1. Forest

Most above-ground biomass equations for forests were developed from fieldwork in Indonesia (n = 18), Vietnam (17), Thailand (11), Southern China (10), Cambodia (8), Malaysia (5), and Papua New Guinea (1) (Tables 1; S1). Of the 17 above-ground equations from Vietnam, all were multi-species apart from two. In addition, 12 of these 17 equations were developed for tropical forests in one or two districts (Table S1), and were hence quite localized.

The relatively large number of equations for Vietnam is due to the efforts of six institutions in Vietnam, working to create a national database as part of the UN REDD+ program (Phuong et al., 2012a). For Thailand, seven equations were multi-species versus four species-specific ones. Multi-species equations include those for dry evergreen, monsoon and mixed deciduous forests (Ogawa et al., 1965; Sabhasri et al., 1968; Viriyabuncha et al., 1996); species-specific equations were all developed for an evergreen forest in Nakhon Ratchasima, Thailand (Sabhasri et al., 1968). Of the 18 above-ground equations from Indonesia, four were species-specific and three were developed in a dry land forest (Krisnawati et al., 2012). Multi-species equations were available for lowland dipterocarp forest (Basuki et al., 2009), mixed dipterocarp forest (Samalca, 2007), lowland evergreen forest (Yamakura et al., 1986), heath forest (Miyamoto et al., 2007; Krisnawati et al., 2012) and dry land forest (Krisnawati et al., 2012).

For Southern China, the five multi-species equations were for a seasonal rainforest (Feng et al., 1998; Zheng et al., 2000; Lü et al., 2010), a monsoon rainforest over limestone (Qi and Tang, 2008), and a tropical mountain rainforest (Huang et al., 1991). The remaining five species-specific equations were developed in a monsoon rainforest over limestone in Xishuangbanna (Qi and Tang, 2008). Cambodia and Malaysia had a total of seven multi-species equations, originating from deciduous, dipterocarp,

evergreen and lowland forests (Table S1). Only one case study in Papua New Guinea developed a site-specific equation for a montane rainforest (Edwards and Grubb, 1977). The number of trees sampled for multi-species equations range from 28 for 21 species in a tropical wet seasonal rainforest in Xishuangbanna (Feng et al., 1998) to 509 trees for 66 species in the tropics and subtropics (Kiyono et al., 2010; Table S1).

To overcome sampling and geographical limitations of site-specific equations, a few researchers developed equations from re-analyzing data from prior studies that did destructive sampling. For example, the pan-tropical equations by Chave et al. (2014) resulted from compiling data from 4004 trees from 58 sites worldwide (diameter range: 5–212 cm). Similarly, 2410 trees from 27 study sites across the tropics (diameter range = 5–156 cm) were re-analyzed by Chave et al. (2005). In all, we found 12 equations developed for the tropics in general including one for lianas (Tables 1, S1). Overall, 74% of all equations were multi-species equations, reflecting the heterogeneous nature of the forest land cover category (Table 3). The remaining equations were species-specific equations, determined for a handful of non-plantation species, such as *Celtis wightii*, *Hopea ferra* and *Hydnocarpus ilicifolius*.

Wood density was regularly included as a variable in above-ground allometric equations in Indonesia and Vietnam, being found in eight of 18 and nine of 17 equations, respectively. However, it was only used in five other case studies (Table S1): Brown et al. (1989), Chave et al. (2005, 2014), Culmsee et al. (2010) and Kiyono et al. (2010). Wood density values were derived from direct sampling in the Indonesian and Vietnamese studies (Basuki et al., 2009; Phuong et al., 2012a); however, of the five other studies, only Brown et al. (1989) derived wood density from direct sampling. Culmsee et al. (2010) and Kiyono et al. (2010) relied on published data. The origin of wood density values for Chave et al. (2005, 2014) and Krisnawati et al. (2012) were unclear.

Only 16 allometric equations were found for root biomass in forests (Table 2). Most were developed in Southern China (9), with only a few developed in three other countries: Cambodia (2), Indonesia (1), Malaysia (1) and Thailand (1). About 69% of these 16 equations were developed from sampling multiple tree species (Table 3). In addition, Mokany et al. (2006) and Cairns et al. (1997) developed two separate equations that could be applied generally to tropical regions (Table S2). In the studies we reviewed, a range of three to 509 trees were sampled for determination of the below-ground equations (Ogawa et al., 1965; Kiyono et al., 2010). Only Kiyono et al. (2010) included wood density as an independent variable in a below-ground equation.

104 above-ground stem volume equations were found – 80 for Indonesia 20 for Cambodia and four for Vietnam. 95% of the Cambodia equations were multi-species equations for tree species in a tropical dry forest, a tropical moist deciduous forest and a tropical rainforest (Forestry Administration, 2004), with the origin of two multi-species equations unclear (United States Agency for International Development, 1962). Meanwhile, one species-specific equation was available for *Anisoptera glabra* (Forestry Administration, 2004). Four multi-species volume equations were found for evergreen broadleaf forests in four separate locations across Vietnam (Dung et al., 2012; Hung et al., 2012a; Huy et al., 2012). The number of trees sampled for developing stem-volume equations range from four to 2932 (Table S3).

4.2. Peat swamp forest

The only above-ground biomass equations for peat swamp forest were reported for Indonesia (14) and Malaysia (1). A total of 148 trees were sampled by Manuri et al. (2014) at three locations in Sumatra and West Kalimantan. Istomo (2006) did not state the number of trees they sampled in Sumatra (Tables 1, S1). Manuri

et al. (2014) used wood density as an independent variable, together with tree diameter and height, in the equation development (Table S1). Three below-ground allometric equations were found for peat swamp forests, two for Indonesia and one for Malaysia (Table 2).

Given the limited availability of equations for peat swamp forests, most case studies estimating biomass have applied pre-existing equations, determined from other forest types. Verwer and van der Meer (2010), for example, applied an allometric equation from lowland mixed dipterocarp forest in East Kalimantan (Basuki et al., 2009) to estimate above-ground biomass in peat swamp forest communities in Sarawak and Brunei. While the equation included several dominant tree genera found in the peat swamp forest type, accuracy of the estimate is not known. Similarly, peat swamp forest biomass has been estimated using the pan-tropical forest equation of Chave et al. (2005), but the various forest types used to develop this equation do not appear to include peat swamp forest species *per se* (Morel et al., 2011; Kronseder et al., 2012).

4.3. Mangrove

Most of the above-ground biomass equations for mangroves originate from Indonesia (n = 19) Thailand (12) and Vietnam (7) (Tables 1, S1). Of the 19 Indonesian mangrove equations, four were developed jointly from fieldwork in Indonesia and Thailand (Poungparn et al., 2003; Komiyama et al., 2005). Four and three equations each were developed in Malaysia and the Philippines. Two originate from Hainan Island in southern China. Only one case study (Thant et al., 2012) reported equations for estimating above-ground biomass in Myanmar, a country where large tracts of mangroves had been destroyed recently for agricultural expansion (Webb et al., 2014). One equation for moist mangrove stands was developed for "tropical regions" by Chave et al. (2005) (Tables 1, S1). In all, we found 45 different allometric equations for estimating above-ground biomass in mangrove ecosystems (Table 3).

Nearly all mangrove equations were species-specific, developed for particular mangrove species such as *Avicennia marina* or *Rhizophora apiculata*. Tree age was known for 12% of equations (Table 3). The most common mangrove species sampled was *Rhizophora apiculata*, with 10 case studies reporting above-ground biomass equations. Five equations were found for *Rhizophora mucronata*. For other species, such as *Avicennia marina* or *Ceriops tagal*, one to three above-ground equations were found in the literature (Table S1). For species-specific above-ground equations, the total number of trees sampled ranged from five *Rhizophora apiculata* trees (Kusmana et al., 1992) to 73 *Rhizophora apiculata* trees (Ong et al., 2004). For multi-species equations, only eight equations were available (Table S1) and only those by Thant et al. (2012) were age-specific. Of these eight equations, sample number ranged from nine trees representing six mangrove species to 104 trees representing ten mangrove species (Table S1). The lack of multi-species equations stems from the fact that there is typically only a few distinct mangrove species present in most mangrove ecosystems (FAO, 1985). Thus, many field investigations estimating carbon biomass in mangroves simply apply to all trees either generalized equations or equations for the dominant species at the site (Chave et al., 2005).

In comparison, only 19 equations were available for estimating below-ground root biomass in mangroves. About two-thirds of these equations were developed in Indonesia (7) and Thailand (5). Malaysia, Myanmar, Southern China and Vietnam contributed one to three below-ground equations each (Tables 2; S2). About two-thirds of the 19 equations were species-specific, while only two were age-specific/single species equations (Table 3). For *Rhizophora* sp., prop roots above the soil surface were always

considered to be part of above-ground biomass. The number of trees sampled for root allometry ranged from one to 47 trees (Poungparn et al., 2004; Dharmawan and Siregar, 2008; Table S2). For both above- and below-ground equations, only the studies of Chave et al. (2005), Komiyama et al. (2005) and Thant et al. (2012) included wood density as an independent variable (Table S1).

16 stem volume equations were found for mangroves: 11 for Indonesia and two to three for Cambodia and Thailand respectively. The three volume equations for Thailand were developed from fieldwork in both Indonesia and Thailand (Poungparn et al., 2003). 56% of these volume equations were species-specific with five to 50 *Rhizophora apiculata* trees sampled (Table S3).

4.4. Logged-over forest

Above-ground biomass equations for logged-over forests were developed for five countries (Tables 1, S1): Indonesia ($n = 22$), Southern China (11), Malaysia (3), Vietnam (3) and Cambodia (1). One of the Malaysian equations was for estimating liana stem biomass (Addo-Fordjour and Rahmad, 2013; Tables 1, S1). Six of the 11 Chinese equations and 10 of the 22 Indonesian equations were species-specific equations. Like forests, only a limited number of species could be enumerated, including *Baccaurea ramiflora*, *Macaranga gigantean* and *Piper aduncum*. For such species-specific equations, the number of trees sampled ranged from three to 56 (Tang et al., 2003, Krisnawati et al., 2012). The age of vegetation was available for seven out of 24 multi-species equations. For multi-species equations, the number of trees sampled range from five to 530 (Hendri et al., 2012; Kiyono et al., 2011) (Table S1). Wood density was included as an independent variable in three studies (Ketterings et al., 2001; Kiyono et al., 2010, 2011).

The number of available below-ground equations was about half the number of above-ground biomass equation—there were 11 for Southern China and three for Cambodia and Indonesia (Table 2). 43% of below-ground biomass equations were species-specific, whereas 29% were age-specific/multi-species equations. The remaining 29% were multi-species equations with no information available for the age of vegetation (Table 3). Where information was available, the number of trees sampled for root biomass equations ranged from three to 509 (Tang et al., 2003; Kiyono et al., 2010; Table S2). Wood density was used only by Kiyono et al. (2010) for estimating above- and below-ground biomass in forests in Cambodia.

4.5. Orchard and tree plantation

Of all the land covers reviewed, orchard and tree plantations had the most number of allometric equations for estimating above- and below-ground biomass (Tables 1, S1, S2): 145 for above-ground biomass and 69 for below-ground biomass. Most of the published above-ground biomass equations were developed in Indonesia ($n = 76$), Thailand (25), Philippines (23) and Malaysia (10). The remaining equations were split almost equally amongst Vietnam (4), Myanmar (3), Lao PDR (2) and Papua New Guinea (2) (Table 1). For root biomass, Indonesia had the most number of equations (44), followed by Thailand (14), Malaysia (6), Lao PDR (2), Philippines (2) and Papua New Guinea (1) (Table 2). Given the homogeneous nature of orchards and plantations, all but two published equations were species-specific, including those for *Acacia mangium*, *Gmelina arborea*, teak (*Tectona grandis*), and coffee (Table S1, S2). Multi-species equations by Kiyono et al. (2007) and Oo et al. (2006) were used for planted tree species commonly found in tree plantations (e.g., *Acacia catechu* and *Eucalyptus camaldulensis*).

As trees in a plantation tend to be of a similar age, age-specific/single-species equations were often developed—45% of the reviewed above-ground biomass equations were of this type, while 55% of below-ground biomass equations were of this type (Table 3). Case studies that sampled fewer than ten trees for developing equations were common. For instance, Yamada et al. (2000) sampled only four *Acacia mangium* trees in Sonbe, Vietnam. Hiratsuka et al. (2005) and Meunpong et al. (2010) sampled only five teak trees at their field sites in Thailand (Table S1). A similar pattern occurs for the development of several below-ground equations: e.g., Kamo et al. (2008) sampled only four trees per species, while Heryati et al. (2011a) sampled five *Hopea odorata* trees (Table S2). Wood density was included in above-ground biomass equations in only the studies of Kiyono et al. (2007) and Oo et al. (2006).

Volume equations were available for Indonesia (70), Malaysia (6), Cambodia (2), Thailand (2) and Vietnam (1). All volume equations were species-specific except for three cases (Table S3).

4.6. Rubber plantation

Eight above-ground biomass equations were available for rubber (Tables 1, S1): two were from Indonesia, two were from Malaysia and the remaining four were from Southern China. Only two equations were available for estimating root biomass (Tables 2, S2) and four for estimating stem volume (Table S3). All published equations were considered species-specific (i.e., for *Hevea brasiliensis*, in general), even though different clones had been studied (Templeton, 1968). Clones were distinguished in Tables S1 and S3. Ages of rubber trees were available for 50% of the above-ground biomass equations and 75% of the volume equations (Table 3). Only three rubber trees were sampled by Tang et al. (2003) for above-ground allometry. In comparison, 30 trees were used in their later study (Tang et al., 2009). The two case studies reporting below-ground equations for root biomass sampled three and 30 trees, respectively, in Xishuangbanna (Tang et al., 2003, 2009; Table S2).

4.7. Oil palm plantation

The different physiological makeup of an oil palm dictates that tree height is more useful as an independent variable than diameter in above-ground biomass estimations (Table S1). Three out of six reported case studies used palm height as the sole independent variable in their allometric equation. An exception was Henson and Dolmat (2003), who used palm age as an independent variable (Table S1). Above-ground biomass equations for oil palm were developed in Indonesia ($n = 3$) and Malaysia (3). Only Henson and Dolmat (2003) developed equations for root biomass, in Malaysia (Table S2). Like rubber, oil palm equations were all considered species-specific (regardless of clone variant). Two out of six case studies reported age-specific above-ground equations (Khalid et al., 1999; Henson and Dolmat, 2003; Table 3). Khalid et al. (1999) reported a sampling quantity of 10 for the determination of their above-ground biomass allometric equation. Eleven palms were cut for the root biomass equation by Henson and Dolmat (2003) (Table S1, S2).

4.8. Bamboo

We found 30 allometric equations for estimating bamboo above-ground biomass. The most equations were determined in Myanmar ($n = 7$) and Vietnam (7), followed by Malaysia (5), Philippines (4), Thailand (4), Lao PDR (2) and Indonesia (1) (Tables 1, S1). Of the 30, only three were multi-species equations that could be applied to more than one type of bamboo (Viriyabuncha et al., 1996; Descloux et al., 2011). The remaining 27 were derived for specific bamboo species. Of the 27 species-specific equations, four were age-specific (Table 3). Bamboo species that had allometric

equations include *Bambusa tulda*, *Gigantochloa scortechinii* and *Schizostachyum zollingeri* – species commonly found in SE Asia. For equation development, Fukushima et al. (2007) and Chan et al. (2013) sampled only five culms of *Cephalostachum pergracile* and *Gigantochola nigrociliata*, respectively. In contrast, Ly et al. (2012) cut 131 culms of *Dendrocalamus barbatus* while Hung et al. (2012c) sampled 120 *Bambusa Chirostachyoides* culms. The multi-species equations by Viriyabuncha et al. (1996) and Descloux et al. (2011) were determined by sampling nine culms from six species and nine culms per size class (total number unclear) respectively (Table S1). No equations for estimating below-ground biomass of bamboo were found in the literature. Lastly, four equations for estimating culm volumes of *Bambusa blumeana*, *Gigantochloa scortechinii*, *Schizostachyum grande* and *Schizostachyum zollingeri* were found with 26 *Bambusa blumeana* to 173 *Gigantochloa scortechinii* culms sampled (Azmy et al., 1991; Table S3).

4.9. Swidden fallow of any length

A total of 28 allometric equations were found for estimating above-ground biomass in swidden fallows. Ten originate from Malaysia. Eight each were determined in Indonesia and Southern China. Lao PDR and Myanmar contributed one equation each (Tables 1, S1). Reflecting the heterogeneous nature of the land cover, 14% of the equations were multi-species equations and another 25% were age-specific/multi-species equations. The multi-species equations represent fallows at various stages of forest regeneration. To develop multi-species equations, Kiyono and Hastaniah (2005) harvested only 14 trees for above-ground allometry in a 34-year fallow (regenerated secondary forest) in Indonesia. Similarly, Ohtsuka (2001) cut 11 trees in Sabah (Insular Malaysia) to develop allometric equations to estimate stem and leaf biomass in a 10-year forest community following shifting cultivation. In contrast, Hashimoto et al. (2004) harvested 191 trees to develop an above-ground biomass equation for a tropical fallow forest in East Kalimantan. In comparison, Chan et al. (2013) harvested up to 160 trees to develop equations for estimating tree above-ground biomass in swidden cultivation fallows in the Bago Mountains of Myanmar (Table S1).

Sixty percent of the equations were species-specific, of which 46% had information on vegetation age (Table 3). Age could be included in many equations because records of fallow lengths were usually reported, as studies were often focused on lengths of cropping and fallow phases of shifting agriculture. Species sampled included *Callicarpa pentandra* (beautyberry) and *Dillenia suffruiticosa* (a large evergreen shrub) growing on abandoned shifting cultivation land in Malaysia (Lim, 1991; Kueh et al., 2014). Small trees or shrubs, including *Apodytes dimidiate*, *Eurya groffii* and *Macaranga denticulate*, were found on swidden land following slash-and-burn agriculture in Xishuangbanna, Yunnan province, China (Shi et al., 2001). The large number of species-specific equations in a supposedly heterogeneous land cover may be due to the fact that a small number of dominant pioneer species occurring on fallow lands facilitates sampling for equation development. Besides age, McNicol et al. (2015) found that plants in swidden fallows can be partitioned according to whether it was re-grown from a seed (simple trees) or re-sprouted from a root stock after being cut (re-sprouting trees). Separate equations were developed for both simple and re-sprouting trees and root biomass was 58% higher after distinguishing between both types of plants.

A total of 14 equations were found for below-ground biomass of swidden fallows. Eight of these were from Southern China; five were from Malaysia and one from Lao PDR. Of the 14 equations, 7% were multi-species, 43% were age-specific/multi-species equations, and the remaining 50% were age-specific/single species

equations (Tables 2 and 3). All but one of the eight equations originating from Southern China was species-specific equations. All five equations from Malaysia were derived from mixed-species fallows. Overall, nine to 91 trees were uprooted to develop root biomass allometric equations for this land cover (cf. Kenzo et al., 2010; McNicol et al., 2015; Table S2). The sole volume equation for this land cover was from a 34 year fallowed secondary forest (Kiyono and Hastaniah, 2005; Table S3).

4.10. Grassland, pasture and shrub land

All three equations for the grassland, pasture and shrubland covers were developed for estimating above-ground shrub biomass (Tables 1, S1). The lack of equations may be related to the ease of determining grass biomass by destructive sampling when estimates were needed (Kamnalrut and Evenson, 1992; Oo et al., 2006; Kamo et al., 2008). Two of the three equations that were species-specific were for *Chromolaena odorata* (L.) and *Melastoma sanguineum Sims*. Both species-specific equations originate from Chieng Khoi watershed in Vietnam, where five and four shrubs were sampled, respectively. From Myanmar, the multi-species shrub/grass equation of Oo et al. (2006) was modified from Kiyono et al. (2004) for use in their study (Tables 1 and 3, S1). No allometric equation for estimating root biomass was found for this cover type.

4.11. Non-swidden agroforest and permanent cropland

No above- or below-ground equations were found for either non-swidden agroforest or permanent cropland land covers (Tables 1 and 2). The lack of equations for permanent croplands results because crops can be easily sampled destructively for biomass determination (Roder et al., 1997; Watcharapirak and Pattanakiat, 2009; Vicharnakorn et al., 2014). In comparison, the lack of allometric equations for agroforests is an artifact of many agroforest trees being common species in tree plantations (eg. cocoa, coffee and rubber), such that pre-existing equations for these plants can be applied (Tomich et al., 1998; Smiley and Kroschel, 2008; Labata et al., 2012). However, given that trees planted alongside crops prevent erosion and help improve poor soils (Budiadi et al., 2006), it is possible that the better soil conditions in agroforestry systems allow tree biomass to be higher than those grown in monoculture plantations (Budiadi and Ishii, 2010). Thus, it is not known if pre-existing equations developed in other land covers estimate biomass of agroforest trees correctly—this issue is complicated because the plant diversity of agroforest vegetation can be highly variable (Rerkasem et al., 2009).

5. Discussion

As tree species and characteristics vary from site to site, pre-existing equations developed at locations that are different from the one in consideration may have limited applicability, even if the equation is species-specific. In addition, many equations are simply "snapshots" of biomass associated with a particular time of the year—e.g., wet or dry period, or periods when leaf shedding is not occurring. In situations where equations were created for a specific conservation project, the equations may be derived from felling a small number of trees (often with disproportionally small biomass) from a limited area (Ketterings et al., 2001). According to Chave et al. (2004), fewer than 50 trees are usually harvested in any field sampling project. For below-ground biomass, underestimates commonly occur as roots are sampled to inadequate depths, large roots are not sampled sufficiently, and roots are lost during sampling and washing (Niiyama et al., 2010; Yuen et al., 2013).

Most equations for above-ground biomass, or biomass of any component (stem, branch, leaves, other) use equations with diameter and/or height as independent variables. Wood density has rarely been included as an independent variable in allometric equations, even though it describes biomass and carbon storage per unit volume of stem (Chave et al., 2004). Other variables such as girth, basal area and crown dimensions have been used even less frequently—usually in special cases. In the case of wood density, using pre-existing values from the literature or databases creates a source of uncertainty that can only be addressed by sampling at the site in question. These issues are explored below, building on the background information presented in Section 2.

5.1. Allometric equation development

We found a total of 402 allometric equations for estimating above-ground biomass and 138 for estimating below-ground biomass (Tables 1 and 2). Of the 12 land covers reviewed, there were few or no above-ground biomass equations for the following land-cover types: rubber and oil palm plantations; grassland, pasture and shrub land; non-swidden agroforest; and permanent cropland in SE Asia. There were few or no below-ground equations for peat swamp forest; rubber and oil palm plantations; bamboo; grassland, pasture and shrub land; non-swidden agroforest; and permanent cropland in SE Asia. The disproportionately low number of below-ground equations results from difficulties associated with sampling roots – the need for labor and machinery to excavate roots often prevents on-site biomass estimates. Consequently, most below-ground assessments must rely on pre-existing allometric equations that may not be representative of site conditions. If root biomass is ignored in carbon accounting projects, an important source of the terrestrial carbon budget will not be accounted for (Yuen et al., 2013). When pre-existing equations are applied, the accuracy is uncertain unless a subset of trees is harvested from the field site for validation of the equation (cf. Thant et al., 2012). However, this extra step is rarely implemented.

When estimating above- and below-ground biomass by allometry, site-specific equations are preferred because tree dimensions and wood density, variables that control biomass, are strongly affected by site-specific geographical variables, including soil properties, land-use history, altitude, and climatic variables including temperature and rainfall (Turnbull, 1948; Barnes et al., 1977; Brown et al., 1989). The following example demonstrates this point with respect to soil conditions. Exotic trees (*Khaya ivorensis*) planted in three different Ultisol series (Padang Besear, Durian and Rengam) in Johor, Malaysia, had very different age-specific diameters, heights, and crown area dimensions. Separate allometric equations were therefore created for each soil type (Heryati et al., 2011b). The sum of above and below-ground biomass was much higher in the Padang Besar soil series (63 Mg/ha), compared with Durian (46 Mg/ha) and Rengam (41 Mg/ha) soil series.

Seasonality is another factor affecting biomass, particularly if leaf shedding occurs—for example, in rubber and teak plantations. Thus, separate equations for leaf-on and leaf-off conditions are needed at different times of the year (Kamo et al., 2008; Chan et al., 2013). This is a common problem for deciduous trees in general. In many cases, changes in tree morphology related to geophysical conditions should be considered before applying an existing equation. Elevation, for example, influences growth rate and total biomass accumulation. Song and Zhang (2010), for example, created separate equations for rubber trees growing at two different elevation ranges. They found that above-ground biomass of 26-year rubber trees growing at 550–600 m was twice that of trees growing at 950–1050 m—high elevations with cool climates that limit rubber growth.

Similarly, differences in precipitation can potentially result in substantial differences in biomass at different sites. To account for this, Brown (1997) and Chave et al. (2005) developed three separate equations for dry forests (precipitation < 1500 mm/year), moist forests (1500–4000 mm/year; the upper bound was 3500 mm/year for Chave et al., 2005) and wet forests (>4000 mm/year; >3500 mm for Chave et al., 2005). Differences in precipitation may also result in substantial differences in growth rates for various species. For example, above-ground biomass of a 38 year old planted *Tectona grandis* forest at a location in Myanmar, with a mean annual precipitation of 1500 mm, was 14 Mg/ha higher than a similar forest growing at a location with 500 mm of rain/year (Kiyono et al., 2007).

Ideally, species-specific equations should be developed and applied to estimate stand-level biomass, but this is unlikely to be possible for all tree species. One approach for overcoming this issue is to construct multi-species equations for specific groups. Species can be grouped according to well-documented traits such as life-history, morphological and physiological traits, and/or dynamic properties such as growth, mortality and recruitment rates (Lavorel et al., 1997; Gourlet-Fleury et al., 2005). The underlying rationale here is that species with similar characteristics are expected to exhibit similar growth patterns, and hence relationships between biomass and stem diameter. A simple grouping would be a binary pioneer/non-pioneer classification using data on seed germination and seedling establishment rates (Swaine and Whitmore, 1988). Taxonomic groupings are not advisable due to poor correlation between the taxonomic group of a tree species and its ecological functioning (Swaine and Whitmore, 1988; Vanclay, 1991a,b; Gitay et al., 1999).

A number of multivariate statistical techniques have been used to group species according to data for a set of characteristics. Commonly, the data are transformed to reduce the dimensionality of the data and perhaps also to remove colinearity among variables, for example via Canonical Discriminant Analysis or Principal Component Analysis. Afterwards, a clustering algorithm is applied to the transformed data using a measure of distance between species characteristics, such as average linkage, complete linkage, or Ward's minimum variance (e.g., Atta-Boateng and Moser, 1998; Gitay et al., 1999; Phillips et al., 2002; Picard and Franc, 2003). An issue shared by all clustering algorithms is that the clusters are defined according to a level of similarity that is essentially arbitrary, which contributes to the lack of congruence in groupings of tree species found in studies of mixed tropical forests (Gourlet-Fleury et al., 2005). In light of this, multi-species equations should ideally be developed for groups of species that are defined using the same methodology. The clustering methods devised by Vanclay (1991a,b, 1992) have the additional problem that the series of significance tests performed to define clusters may result in high type I error (Vanclay, 1991b).

We found agreement among reviewed studies that the (near) largest and smallest trees present at the research site should be included in developing the equations. However, there was no consensus on the quantity of trees that should be sampled. Sample numbers were often decided based on resource availability, even though sampling quantity should be determined by the range of tree diameters present and the distribution of trees in each diameter class. We found case studies that sampled only 3–5 trees (cf. Kusmana et al., 1992; Tang et al., 2003; Phongoudome et al., 2012). It is unclear, however, if these trees were representative of all trees at the site, thereby justifying the small sample number. Roxburgh et al. (2015) found that for 23 power-law equations relating above-ground biomass to diameter for tree species in southeastern Australia, sample sizes of 17–166 were required to achieve a coefficient of variation of stand-level above-ground biomass predictions lower than or equal to 0.05. This suggests that

sample sizes should be greater than 3–5 to achieve accurate biomass estimates. In particular, Roxburgh et al. (2015) found that it was important to match the diameter distribution of the trees used to derive an equation and the diameter distribution of trees to which the equation is applied. Furthermore, sampled trees should be randomly selected, regardless of health condition or degree of damage, because sampling only trees with fully intact structural characteristics will likely result in an equation that over estimates biomass for the general case (Chambers et al., 2001). In this respect, data outliers should not be removed simply to improve model fit metrics.

Following on from the discussion in Section 2, there are now a wide variety of statistical models that can be used to fit data for estimating the biomass of trees. However, studies rarely test for the normality and homoscedasticity of errors in these models—steps that are essential in deciding the appropriateness of a model. In addition, when using ordinary least squares regression, multicollinearity of explanatory variables should be tested to avoid inaccurate and imprecise parameter estimates (Section 2). Thus, it is recommended that future studies of tree biomass estimation ensure that rigorous tests of underlying model assumptions are performed (and the results reported). Similarly, standard errors and confidence intervals that can be derived from models were rarely reported in the studies reviewed. Therefore, uncertainty in parameter estimates should also be reported thoroughly and incorporated into biomass estimates.

A related issue is that model fitting typically treats values of explanatory variables as known without error, whereas in reality they have measurement error. This type of error can be random or systematic, and can arise from measurement inconsistencies, data recording errors, and data entry errors (Cunia, 1987a; Muller-Landau et al., 2014). Screened outliers resulting from measurement error can be removed or corrected using methods such as interpolation. For example, when a tree community has individuals with buttresses, a particularly important type of measurement error is failure to account for measuring above the standard measurement height (Muller-Landau et al., 2014). Because trees typically taper with height, a buttressed tree would have a smaller measured diameter than a non-buttressed tree of the same biomass. Therefore, allometric biomass equations derived using buttressed trees would give overestimates of biomass when applied to unbuttressed trees. Taper equations can be used to correct measured diameters for buttressed trees and hence reduce the corresponding measurement errors (Cushman et al., 2014). In addition, for large tree components that are hard to measure, subsampling schemes are often used to derive estimates of trait values (Parresol, 1999), resulting in the potential for large measurement errors.

5.2. Wood density

Studies on harvested trees show that wood density is an important variable for predicting tree biomass with allometry (Chave et al., 2005). When wood density is taken into consideration, the trees with the largest diameters do not necessarily have the highest biomass. In a lowland dipterocarp forest in East Kalimantan, for example, a *Shorea superba* tree with a diameter of 170 cm had a corresponding above-ground biomass (40 Mg) that was higher than another *Shorea sp.* tree with a diameter of 200 cm (36 Mg). Differences in wood density partially explain this difference (Basuki et al., 2009): the wood densities were 0.86 g/cm^3 and 0.57 g/cm^3, respectively. Further, the relationship between heights was opposite (26 m for *Shorea superba* versus 28 m for *Shorea sp.*).

Wood densities are required when stem biomass is calculated from stem volume. Of the studies reviewed, only 26 included wood density in their allometric equations—all but six were published

after 2005. Also, the prevalence of using pre-existing equations that excluded wood density (e.g. Brown, 1997) means that an important determinant of biomass has not been taken into consideration in many studies. The lack of studies could be due to the fact that extra effort and resources are needed to measure the wood density of all trees.

Wood density is strongly influenced by environmental factors such as soil fertility, natural disturbance frequency, light availability, humidity and climatic zone (Turnbull, 1948; Barnes et al., 1977; Chave et al., 2004; Nogueira et al., 2007). As such, the same species of tree growing in different locations can have different wood densities. For example, when wood densities of trees in the "arc of deforestation" (encompassing the southwestern, southern and eastern edge of the Amazon basin) were compared to published values taken from trees outside the arc, the differences were sufficient to produce important over-estimates of biomass. The mean wood density for southern and southwest Brazilian Amazon was 0.583 g/cm^3, which was 8–22% lower than published estimates. Thus, the wood density value for the entire Amazon region needed to be reduced 7%, from 0.69 g/cm^3 to 0.64 g/cm^3, to produce reliable estimates.

For many published values, it is not known how wood densities were derived or if radial or longitudinal variations along the stem were taken into consideration (Williamson and Wiemann, 2010; Swenson and Enquist, 2008). Fig. 1 illustrates the differences in cumulative above-ground biomass per tree in a study plot when measured versus pre-existing wood density values were used to estimate above-ground biomass (see information in Table 4). The values were determined within a 20 × 20 m plot in an evergreen forest at the Pong Khrai Royal Forest Department Research station (18°54′N and 098°48′E), in Chiang Mai province of northern Thailand (collected to support this review). Within the plot, trees ⩾5 cm DBH were assessed. Wood cores were collected with a 0.200 in. diameter tree increment borer. Wood density was determined following Dietz and Kuyah (2011). Above-ground biomass was estimated with the equation of Chave et al. (2005) for dry forest stands. The mean measured wood density was 0.75 g/cm^3 compared with a published value of 0.62 g/cm^3. These differences produced substantial above-ground biomass estimate differences, equivalent to 31 Mg/ha (Fig. 1).

This example demonstrates the importance of measuring density *in situ* rather than relying on pre-existing values. Environmental variations and the presence of hollows, internal defects,
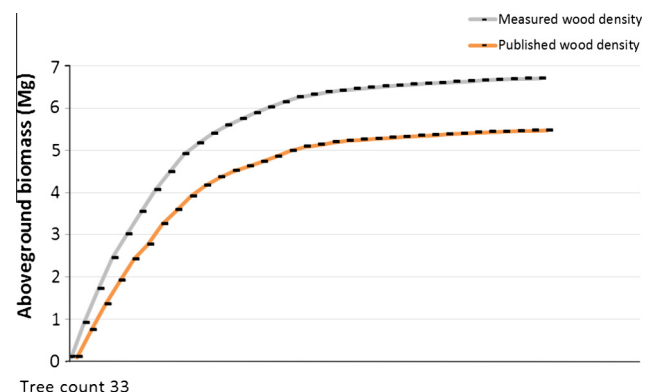
Fig. 1. Cumulative above-ground biomass (AGB) for 33 trees in a 20 × 20 m plot in an evergreen forest at the Pong Khrai Royal Forest Department Research station (18°54′N and 098°48′E), in Chiang Mai province of northern Thailand. AGB was determined using Chave et al. (2005)'s allometric equation for dry forest stands (Table S1) and measured versus published wood density values. Trees were ordered, left to right, from the largest to smallest biomass, with each tree represented by a black horizontal line in each plot.

Table 4

Comparison of above-ground biomass estimates determined from measured versus published wood density values for 33 trees in a 20 × 20 m plot in an evergreen forest in Chiang Mai, Thailand.

Tree no.[*]	Species	DBH (cm)	Measured wood density (g/cm^3)	Published wood density (g/cm^3)	AGB (kg) – measured wood density[**]	AGB (kg) – published wood density[**]	Note[***]
1	*Albizia odoratissima* (L.f.) Benth	30.3	0.68	0.62	556	508	1
2	*Croton roxburghii* N.P.Balakr	5.5	0.65	0.57	11	10	3
3	*Shorea roxburghii* G.Don	6.9	0.67	0.70	19	20	1
4A	*Adenanthera microsperma* Teijsm. & Binn.	29.9	0.84	0.64	669	511	1
4B	*Adenanthera microsperma* Teijsm. & Binn.	11.0	0.84	0.64	69	53	1
5A	*Adenanthera microsperma* Teijsm. & Binn.	24.0	0.79	0.64	387	313	1
5B	*Adenanthera microsperma* Teijsm. & Binn.	23.9	0.79	0.64	383	310	1
5C	*Adenanthera microsperma* Teijsm. & Binn.	15.4	0.79	0.64	141	114	1
6A	*Adenanthera microsperma* Teijsm. & Binn.	24.0	0.84	0.64	411	313	1
6B	*Adenanthera microsperma* Teijsm. & Binn.	23.4	0.84	0.64	388	295	1
7	*Lagerstroemia cochinchinensis* Pierre ex Gagnep	9.1	0.75	0.71	40	38	2
8	*Lagerstroemia cochinchinensis* Pierre ex Gagnep	20.6	0.75	0.71	259	247	2
9	*Croton roxburghii* N.P.Balakr	5.0	0.54	0.57	7	8	3
10	*Apostasia wallichi* R.Br.	6.0	0.71	0.57	15	12	3
11	*Glochidion sphaerogymum* (Müll.Arg.) Kurz	8.0	0.93	0.62	37	25	2
12A	*Turpinia pomifera* (Roxb.) DC.	5.6	0.73	0.45	13	8	1
12B	*Turpinia pomifera* (Roxb.) DC.	6.7	0.73	0.45	20	12	1
13A	*Gmelina arborea* Roxb.	25.4	0.64	0.43	356	238	1
13B	*Gmelina arborea* Roxb.	18.4	0.64	0.43	172	115	1
14	*Glochidion sphaerogymum* (Müll.Arg.) Kurz	16.1	0.71	0.62	140	123	2
15	*Lagerstroemia villosa* Wall. ex Kurz	15.9	0.62	0.69	118	132	1
16	*Canarium subulatum* Guillaumin	29.1	0.68	0.64	514	479	2
17	*Bauhinia variegata* L.	25.0	0.78	0.61	418	324	1
18	*Apostasia wallichi* R.Br.	11.1	0.71	0.57	60	48	3
19	*Croton roxburghii* N.P.Balakr	7.0	0.72	0.57	21	17	3
20	*Lagerstroemia villosa* Wall. ex Kurz	6.1	0.74	0.69	16	15	1
21	*Cratoxylum cochinchinense* (Lour.) Blume	15.2	0.82	0.67	143	116	1
22	*Croton roxburghii* N.P.Balakr	6.1	0.74	0.57	16	12	3
23	*Lagerstroemia villosa* Wall. ex Kurz	7.6	0.67	0.69	24	24	1
24	*Lagerstroemia villosa* Wall. ex Kurz	11.2	0.67	0.69	58	59	1
25	*Lagerstroemia villosa* Wall. ex Kurz	19.0	0.82	0.69	236	198	1
26A	*Glochidion sphaerogymum* (Müll.Arg.) Kurz	14.0	0.71	0.62	102	89	2
26B	*Glochidion sphaerogymum* (Müll.Arg.) Kurz	5.8	0.71	0.62	14	12	2
27A	*Micromelum minutum* (G.Forst.) Wight & Arn.	13.4	0.93	0.66	121	86	1
27B	*Micromelum minutum* (G.Forst.) Wight & Arn.	7.5	0.93	0.66	32	23	1
28	*Cratoxylum cochinchinense* (Lour.) Blume	7.0	0.69	0.67	20	20	1
29	*Glochidion sphaerogymum* (Müll.Arg.) Kurz	7.5	0.77	0.62	26	21	2
30	*Apostasia wallichi* R.Br.	7.8	0.65	0.57	24	21	3
31	*Dalbergia cultrata* Graham ex Benth.	6.4	0.81	0.77	19	18	1
32A	*Glochidion sphaerogymum* (Müll.Arg.) Kurz	9.7	0.74	0.62	45	38	2
32B	*Glochidion sphaerogymum* (Müll.Arg.) Kurz	15.5	0.80	0.62	146	113	2
33	*Glochidion sphaerogymum* (Müll.Arg.) Kurz	25.0	0.81	0.62	434	333	2

[*] Tree numbers that are the same except for different alphabets represent multiple stems. For multi-stemmed trees, wood core was taken from only one stem.

[**] Above-ground biomass (AGB) per tree was estimated with the equation of Chave et al. (2005) for dry forest stands.

[***] Published wood density values are from (1) Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009); (2) Wood Density Database by the World Agroforestry Centre (2014); (3) Brown (1997), which is a default value of 0.57 g/cm^3 that is assigned if no wood density value was found in published databases.

fungal or insect damage affect wood density estimates (Keith et al., 2000). With this example, we draw attention to the fact that wood density values from prior works and published databases (e.g., Global Wood Density Database and the Wood Density Database by the World Agroforestry Centre) are often conveniently used in lieu of actual measurements in biomass studies (cf. Hiratsuka et al., 2005; Verwer and van der Meer, 2010; Rutishauser et al., 2013; Vincent et al., 2015). While we recognize the value of such databases, we advise taking care in interpreting biomass estimates based on wood densities from these databases.

5.3. Height

While in some studies reviewed, stem diameter alone was a good predictor of biomass (e.g., Smith and Whelan, 2006; Banaticla et al., 2007; Kuyah et al., 2012), the inclusion of tree height improved biomass predictions in others (e.g., Chan et al., 2013; Chave et al., 2014). Unless trees are felled, height measurements are not easily obtained in closed canopies (Chave et al., 2005). Remote sensing methods such as light detection and ranging (LiDAR) overcome this difficulty by determining tree

height to within several centimeters. Unfortunately, it is costly and specialized skills are needed for analysis. Consequently, LiDAR has only been used in a limited number of cases (Kronseder et al., 2012; Kuyah et al., 2014). Laser range finders help in the calculation of height from a geometric relationship, but the estimates can have substantial errors, which could ultimately influence equation development (cf. Williams and Schreuder, 2000; Molto et al., 2012; Hunter et al., 2013).

Here, we recall that height can be estimated as a function of diameter at breast height. In this case it is not an independent variable when used in an equation that already has a diameter variable (Sileshi, 2014). In the studies reviewed, we found 50 instances of height-diameter equations. These equations pertain to species in forests, mangroves, logged-over forests, tree plantations, bamboo stands, and swidden fallows, located in SE Asia and Southern China (Table S4). Most of the equations follow a saturating function, whereby height approaches an asymptote as the diameter increases.

As mentioned in the background section above (Section 2), the validity of including height as an independent variable in equations already based on DBH is debatable. This debate is relevant

to our assessment of allometric equations available for biomass determinations in the region. If the goal is to estimate the biomass accurately within any given stand where destructive sampling can be performed, the inclusion of multiple non-independent variables of vegetation characteristics (e.g., DBH, height, density, crown size), as well as the use of any reasonable form of equation, is arguably justifiable to account for the influence of all geographically-influenced growing conditions. Picard et al. (2015) conclude that such models allow one to relate tree-level variations in biomass to stand-level attributes such as stand density, local competition, moisture stress, and nutrient availability (see also Temesgen et al., 2015). For similar reasons, Chave et al. (2014) recommended the development of locally derived diameter–height relationships whenever possible to minimize bias. It is not the intention of this review to assess the validity of including both height and diameter in location-specific or general allometric equations. Rather, we wish to warn of the potential problem resulting from applying any model developed in a particular location or locations to a new setting without first testing if the proposed allometric relationships hold.

5.4. Use of pre-existing equations

Where destructive sampling of biomass is not possible, the use of pre-existing equations is the only method available for biomass estimation (Fox et al., 2010; Ngo et al., 2013; Vicharnakorn et al., 2014; Vincent et al., 2015). This is unfortunately the situation for biomass estimation for land covers in SE Asia with few or no allometric equations (Tables 1 and 2). The study of Manuri et al. (2014) demonstrates the difficulties in using pre-existing equations. At three peat swamp forest sites in Indonesia where 148 trees were harvested, local equations determined by Basuki et al. (2009) and Ketterings et al. (2001) over-estimated above-ground biomass. Similarly, after cutting 108 trees in a lowland dipterocarp forest in East Kalimantan, Rutishauser et al. (2013) found that regional equations by Yamakura et al. (1986) and Basuki et al. (2009) underestimated above-ground biomass by 0–10% and 25–40%, respectively. This point is further shown in a study conducted by Basuki et al. (2009) in a lowland dipterocarp forest in East Kalimantan, Indonesia. When equations by Chave et al. (2005) and Brown (1997) were applied to the data from cutting 122 trees, above-ground biomass was over-estimated. In comparison, biomass was under-estimated when the equation of Ketterings et al. (2001) was applied.

In our prior review of above-ground carbon stocks (Ziegler et al., 2012), at least 30% of the entries for the forest, peat swamp forest, orchard and tree plantation, rubber plantation, oil palm plantation, long-fallow swidden, intermediate-fallow swidden, and non-swidden agroforest categories were derived by applying pre-existing equations to forest plot data. At the high end, 60% of the mangrove and logged-over forest entries were determined from pre-existing allometric equations (Ziegler et al., 2012). The equation by Komiyama et al. (2005) was popular among mangrove studies (Wilson, 2011; Jachowski et al., 2013; Tue et al., 2014) while equations of Brown (1997), Ketterings et al. (2001) and Chave et al. (2005) were commonly used for forested land covers, including peat swamp forests and logged forests. Even for land covers that tend to be homogeneous (e.g. tree plantations) general equations have been applied (e.g., Hairiah et al., 2002; Morel et al., 2011).

Meanwhile, in our prior review of below-ground carbon studies (Yuen et al., 2013), at least 40% of the entries for seven out of 12 land covers (forest, mangrove, logged-over forest, orchard and tree plantation, bamboo, non-swidden agroforest, and permanent cropland) relied on pre-existing equations, including root:shoot ratios. The lack of root research in the region creates the situation where a

few allometric equations have been used repeatedly—for example those by Komiyama et al. (2005) for mangroves and Cairns et al. (1997) for forest trees. As such, it is possible that biomass estimates reported in a large proportion of the case studies reviewed have substantial errors because life forms at the study sites are potentially different from those where the equations were developed (see discussion above). Moving forward, we suggest that when published equations are needed, multiple, potentially applicable allometric equations should be compared, and the ranges of above-ground biomass and below-ground biomass be reported. Again, pre-existing equations should be validated via sampling prior to use—if possible.

Further, biomass estimation error occurs when pre-existing equations are applied to trees having diameters outside those from which the equation was developed (Cunia, 1987b; Nelson et al., 1999; Chave et al., 2004). Error related to model selection may also introduce great uncertainty in live tree carbon estimates (Cunia, 1987b; Chave et al., 2004; Melson et al., 2011). This may be the largest source of error in many estimates. To illustrate these points, three different allometric equations to estimate above-ground biomass were applied to diameters ranging from 1 to 25 cm for *Acacia mangium* (Fig. 2). The three equations for *Acacia mangium* were from Miyakuni et al. (2004), Lim (1988) and Yamada et al. (2000) (all equations shown in Table S1). Above-ground biomass per tree was calculated as the sum of stem, branch, bark and leaves biomasses derived from separate equations. The calculations show that above-ground biomass estimates are greatly different for diameters >15 cm. At 25 cm diameter, the difference between the highest and lowest tree above-ground biomass is 160 kg (Fig. 2). The equations of Lim (1988) are inappropriate for tree diameters beyond 22 cm: at 25 cm DBH, above-ground biomass determined by this equation differs from that calculated with equations of Miyakuni et al. (2004) and Yamada et al. (2000) by 77 and 160 kg, respectively. In addition, although the equations of Yamada et al. (2000) are suitable for trees with diameters ranging from 1 to 26 cm, and $R^2 > 0.95$ are recorded for stem and branch equations, their equations were determined from just four trees—only one of these trees had a diameter greater than 20 cm. This
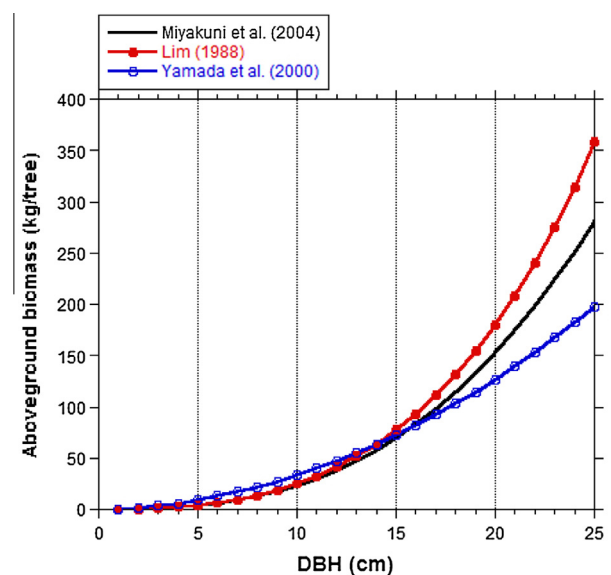

Fig. 2. Differences in above-ground biomass values for *Acacia mangium* trees after applying three different species-specific equations: Miyakuni et al. (2004), Lim (1988) and Yamada et al. (2000). Above-ground biomass estimates were greatly different for DBH values >20 cm, demonstrating how equation choice can produce uncertainty.

example shows that care is needed in biomass estimation projects to ensure that the range of trees in question corresponds with the range from which the equation used was developed.

Finally we draw attention to the GlobAllomeTree database http://www.globallometree.org/data/search/ that lists many equations for Cambodia, Indonesia, and Vietnam. The total number of unique biomass equations listed for the three countries to 5, 5 and 73 (Table S1). The five equations listed for Indonesia originate from the work of Kiyono et al. (2011). The database indicates these equations are viable for 14 different species or genera in Indonesia (*Acacia leucophloea*, *Azadirachta indica*, *Dialium platycephalum*, *Dipterocarpus crinitus*, *Erythrina* spp., *Ficus* spp., *Hopea mengerawan*, *Polyalthia glauca*, *Santiria tomentosa*, *Schleichera oleosa*, *Shorea laevis*, *Sterculia foetida*, *Tamarindus indica*, *Zizyphus rotundifolia*). However, the five equations are also listed for three families of tree in Cambodia (*Anisoptera* spp., *Calophyllum* spp., *Myristica* spp.). The Cambodia equations originate from the work of Kiyono et al. (2011) as well. Many of the Vietnam equations also represent groups of 12–66 tree species or genera. There are also equations for the individual species *Bambusa balcoa*, *Endospermum sinensis*, *Indosasa angustata*, and *Vatica odorata*. In total there are 73 unique biomass equations for Vietnam species. At first glance the database appears to be a valuable resource for performing biomass estimations in SE Asia, but this usefulness is currently undermined by (a) limited representation of all SE Asian countries; (b) inclusion of few non-tree species; and (c) general association of particular species in areas outside where the equations were developed. Thus, caution is needed when using the reported equations without reviewing their source references.

6. Conclusion and future directions

The use of pre-existing allometric equations, rather than equations determined on site, is an important source of uncertainty in assessments of biomass and carbon changes following land cover conversions in SE Asia. It is important to choose representative equations; however, this is often difficult because of the limited amount of work that has been conducted in the region for most important land covers. Where pre-existing equations are needed, multiple, potentially applicable equations should be used to determine plausible ranges of above-ground biomass and below-ground biomass. Ideally, the suitability of the pre-existing equations should be verified by on-site sampling, when permitted.

The studies reviewed offer limited guidance for choosing the most accurate equations for any given land cover. Nevertheless, some insights can be gleaned from the review. For example, it is important that stem diameter and wood density are included as variables in equations for predicting tree-based land cover biomass. Wood density is important for describing biomass/carbon storage in a unit volume of stem. However, using density values determined elsewhere may introduce substantial error in a biomass estimate. As species and physical characteristics vary from site to site, the applicability of equations developed at different locations may also be limited, even if equations are species-specific. While choosing species-specific equations might appear straightforward, site and seasonal conditions of the vegetation used to develop the equations are often variable between sites.

There are also issues that apply to specific types of land cover. Oil palm, for example, is problematic in that it is not clear if age or height is the best indicator of biomass—and these relationships may change with geographic setting. Determination of biomass equations for grassland and shrub land is difficult when diversity is high, preventing the establishment of a robust relationship between height/form and vegetation density, and hence biomass.

Equations for agroforests and younger forms of swidden fallows are similarly challenging, particularly if they also contain larger plants (bamboo, small trees) in addition to shorter vegetation. Rubber represents a challenge for developing accurate biomass equations because its life form varies greatly across the wide range of ideal and marginal physiographic settings where it is now being grown commercially (Ahrends et al., 2015). On the other hand, as many other plants are also affected by variability in physiographic settings, this issue is not necessarily specific to rubber.

Where multi-species equations are used, especially for heterogeneous land covers such as mature forest, it is essential to verify that the species present are similar to those used to develop the original equations. Estimates are also possibly flawed if equations are applied to diameter ranges outside of (especially larger than) those from which they were derived. In addition, estimates for diverse forests may be flawed even if equations for similar species are applied, because of diverse environmental settings that are often associated with SE Asian landscapes. If possible, site-specific equations should be developed from harvesting an appropriate number of trees that encompass the full range of diameter classes present. Sampled trees should also not be limited to only healthy individuals. Currently, there is no consensus on the number of trees that should be sampled, as this is often dependent on resource availability and permission to harvest trees.

Among the many difficulties and problems associated with estimating below-ground root biomass, the use of inaccurate allometric equations could lead to substantial errors in biomass estimates. The current preference (or necessity) for using pre-existing below-ground equations, especially root:shoot ratios, produces uncertainties in below-ground estimates. In general, more below-ground research with an adequate number of replicates sampled to appropriate depths is needed in all land covers. When root sampling is performed, all associated limitations should be acknowledged during reporting to allow comparability with other studies and estimate uncertainty.

Given the sources of uncertainty in biomass estimates identified herein, our meta-analysis raises an important question: How can biomass estimations related to on-going and potential land cover changes in SE Asia be made with high certainty to advise policies/programs (REDD+ and others) when appropriate allometric equations needed to do so are insufficient and/or existing equations are being applied inappropriately? To address this question, research could be better aligned with construction, mining, crop rotation activities and tree fall incidents to increase the quantity of trees available for destructive sampling in important types of land cover, without removing trees from sensitive areas. Further, the need to evaluate and standardize current field methods should be at the heart of REDD+ debates before remote sensing methods are applied to extrapolate carbon stocks over a larger area.

Many of the above points of consideration echo those of other researchers (Brown, 2002; Melson et al., 2011; Qureshi et al., 2012). Importantly, for the purpose of informing the development and implementation of policies and programs such as REDD+, our meta-analysis highlights the pressing need to address the insufficient number of allometric equations and their inappropriate use when estimating vegetation biomass in SE Asia, under current and potential land cover changes.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.09.016.

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