



New allometric equations for quantifying tree biomass and carbon sequestration in seasonally dry secondary forest in northern Thailand

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Abstract

As tropical deforestation and forest degradation accelerate, carbon-credit trading could provide a financial incentive to preserve and regenerate forests. Since carbon trading relies on the accurate quantification of carbon stocks, allometric equations are urgently needed to derive above-ground dry biomass (AGB) from easily measured variables. Few allometric equations have been published for regenerating secondary forests in Southeast Asia. This study established new allometric equations, to determine AGB and carbon in regenerating secondary forests on shifting cultivation fallows in northern Thailand. To develop the equations, data were collected from 78 trees (136 felled individual stems, including coppices) ranging in size from 1 to 32.9 cm diameter at breast height (D). The dependent variable was AGB. The independent variables were D, tree height (H) and wood density (WD). Wood density varied significantly among species ($p < 0.05$). Consequently, including WD in the function $D^2H \times WD$ predicted AGB most accurately, compared with other functions that excluded it. Mean carbon concentration in stems, branches, and leaves was $44.84\% \pm 1.63$ of dry mass, but it varied significantly among tree species ($p < 0.05$). The new allometric equation revealed that tree AGB was highest in secondary forest, followed by the 7-year-fallow and the 4-year-fallow: 105.3, 38.3 and 10.3 Mg ha⁻¹, respectively, while above-ground carbon was 47.7, 17.4, and 4.6 Mg C ha⁻¹, respectively. Natural regeneration accumulated carbon slower than reported for active restoration, suggesting that managed restoration is preferable to passive regeneration on fallows in northern Thailand. The allometric equations, derived from this study, can be used to accurately determine tree AGB and carbon storage in regenerating secondary forest, with higher precision than has hitherto been possible, thus satisfying the monitoring requirements of REDD+ and other carbon-trading schemes.

Keywords Aboveground biomass · Allometric model · Secondary succession · Tropical forest · Wood density

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Introduction

Secondary forests (i.e. forests undergoing regeneration, following logging, shifting cultivation or other disturbances) are rapidly becoming the most common forest type across tropical Southeast Asia (Bruun et al. 2009; Rerkasem et al. 2009; Chazdon 2014). As of 2015, they accounted for about 65% of the region's forest cover, and models predict that they will become even more predominant over the next few decades (Estoque et al. 2019). Such forests have an enormous capacity to remove carbon dioxide from the atmosphere and store it as complex organic molecules in biomass and soil. Consequently, secondary forests could contribute substantially towards climate-change mitigation (Chazdon et al. 2016; Poorter et al. 2016). They also provide forest products, other ecosystem services (such as watershed functions) and wildlife habitats for biodiversity conservation (Rerkasem et al. 2009).

REDD+ (Reducing Emissions from Deforestation and Forest Degradation) comprises policies and incentives, developed under the UN Framework Convention on Climate Change, to finance forest conservation and restoration, by placing a value on the capacity of forests to sequester carbon. Ultimately REDD+ aims to make forest restoration and conservation, for carbon storage, more lucrative than deforestation and other land uses (UNREDD 2016). Originally conceived as a mechanism merely to slow CO₂ emissions from forest destruction, the scheme was subsequently expanded to include "enhancement of carbon stocks" (United Nations 2007) i.e., removal of CO₂ from the atmosphere by forest expansion. This has created new international funding mechanisms that can be used to support forest regeneration e.g. the Green Climate Fund, carbon credits etc. However, to qualify for REDD+, forest regeneration must be carried out with the "full and effective engagement of ... indigenous peoples and local communities". This means that forest regeneration must provide the forest products and ecosystem services, valued by local communities, with minimal impact on local food production, particularly where land tenure is disputed. Secondly, actions must be "consistent with the conservation of natural forests and biological diversity ... and ... incentivize the protection and conservation of natural forests and their ecosystem services and enhance other social and environmental benefits" [United Nations 2007, 2010, safeguards (d) and (e)].

Both of these safeguards can be met through natural forest regeneration. Therefore, many REDD+ projects now focus on secondary forests (Chan et al. 2016; Borah et al. 2018). Consequently, it is becoming increasingly important to accurately quantify carbon accumulation in regenerating forests, in order to calculate payments under REDD+ -related projects (Boissière et al. 2014; Krause and Nielsen 2019).

Since trees cannot be weighed without killing them, ecologists use allometric equations to derive their above-ground dry biomass (ABG) indirectly, via its relationship with easier-to-measure variables [e.g. tree stem diameter at breast height (D) and/or tree height (H)]. Although several such equations have been developed for tropical forests, the parameters used in them and even the form of their functions are specific for forest type and tree species. Few allometric equations have been established for the secondary forests that regenerate following selective logging, forest fires, agriculture abandonment or on fallow land in Southeast Asia (Hashimoto et al. 2000; Ketterings et al. 2001; Hashimoto et al. 2004; Kenzo et al. 2009; Chan et al. 2013; McNicol et al. 2015).

Small trees, which are of course predominant in such forests, have received even less attention, with only a handful of studies that include trees smaller than 5 cm D (Kenzo et al. 2009; Chan et al. 2013; McNicol et al. 2015), saplings (0.4–8.3 cm D) (Noulèkoun et al. 2018). The architecture, traits and biomass allocation of trees, during early forest

succession, often differ from those of older trees in undisturbed or logged-over forests. Furthermore, coppicing tree stumps are common, particularly in regenerating fallow fields (Fukushima et al. 2008; McNicol et al. 2015). Furthermore, wood density (WD) of the fast-growing pioneer tree species, typical of such sites, is usually significantly lower than that of climax tree species (Hashimoto et al. 2004).

Destructive harvesting is the most direct and precise method to measure plant biomass. It involves harvesting all tree components, drying them and then weighing them (Gibbs et al. 2007; Picard et al. 2012). Such techniques are used to develop allometric models, which are subsequently used to predict ABG over large areas (Brown 1997; Basuki et al. 2009). Several allometric models have been developed for tropical forests, based on tree size, as indicated by either by D alone (Brown 1997) or by various functions that combine D with H (Ogawa et al. 1965; Tsutsumi et al. 1983; Kenzo et al. 2009; Chan et al. 2013; McNicol et al. 2015). However, in addition to tree size, wood density (WD) is also important, because it varies considerably among tree species. Consequently, incorporating WD into allometric functions greatly improves the accuracy of AGB determination (Baker et al. 2004; Chave et al. 2005, 2014; Basuki et al. 2009; van Breugel et al. 2011; Chaturvedi et al. 2012; Chaturvedi and Raghubanshi 2013; Fayolle et al. 2013; Huy et al. 2016a, b; Kralicek et al. 2017). However, WD has not yet been incorporated into allometric equations for Southeast Asian forests, particularly for small trees (Kenzo et al. 2009; Chan et al. 2013; McNicol et al. 2015). Consequently, the equations, currently being considered to pave the way for REDD+ implementation in Thailand, are unlikely to provide reliable estimates of the carbon credit value of regenerating forests.

More accurate determination of carbon accumulation, during forest regeneration, would enable the development of the scalable financial incentives that are demanded by REDD+. However, the proper tools and optimal equations for quantifying carbon sequestration by secondary forests, at the landscape level in Thailand, do not yet exist. Clearly, developing allometric equations, based on more complete and accurate data, is an urgently needed prerequisite for implementation of REDD+. Therefore, here, we present original allometric equations, derived from felling trees in secondary forests, regenerating on fallow fields, for more accurate quantification of forest biomass and carbon in northern Thailand. The study included coppicing trees, which are a large component of the secondary re-growth, since they have been rarely included in other studies. This study may be useful for the development of properly financed REDD+ projects, based on carbon sequestration by regenerating secondary forests, not only in Thailand, but also across upland Indochina, where similar conditions prevail.

Materials and methods

Study site

This study was conducted in shifting cultivation areas, near the Lawa community of Ban Ho (18° 27' 24.7" N 98° 10' 51.2" E), Mae Chaem watershed; a sloping highland area, interspersed with narrow valleys in Chiang Mai Province, Thailand. The area is a protected watershed (classified as A1), well known for its high botanical diversity. For generations, highland ethnic communities have practiced various land-use systems, such as paddy fields in the valleys and shifting cultivation or slash and burn on the slope areas (Thomas et al. 2004; Junsongduang et al. 2014). Today, shifting cultivation is being largely replaced

with permanent agriculture. The secondary forest type in this area is classified as seasonally dry evergreen scrub (sensu Maxwell and Elliott 2001) (precipitation < 1500 mm/year, > 5-month dry season) (Brown 1997; Chave et al. 2005). At Mae Chaem District, the mean annual temperature was 26.4 °C, with average annual precipitation of 980 mm (Northern Meteorological Centre, Chiang Mai, 2007–2017).

Three study plots (60 m × 60 m) were divided into three land use categories: 4-year fallow (4Y), 7-year fallow (7Y), and secondary forest (SF) (approximately 50 years old). Each site (4Y, 7Y and SF) was divided into three sampling plots of 20 m × 60 m (1200 m²), resulting in nine plots in total. The sampling plots of each site were drawn parallel to the contour lines in three positions (lower, middle, upper slopes) within 20 m from each other. Elevation ranged from 1050 to 1270 m asl. For many decades, the Lawa community of Ban Ho have practiced shifting cultivation, predominantly growing upland rice. When preparing fallow areas for cultivation, trees are usually cut 1–1.5 m or more above the ground. Some big trees may be left standing as relict emergents, because their thick trunks or hard wood make them difficult to cut; this is a common characteristic in shifting cultivation areas. Coppicing is another regenerative process that is often found on shifting-cultivation fallow sites (Fukushima et al. 2008; Rerkasem et al. 2009; Wangpakapattanawong et al. 2010). In this study, coppicing trees were abundant in the 4Y and 7Y plots. According to the villager elders, the SF was also used for shifting cultivation, but approximately 50 years ago, the villagers ceased cultivation there. That resulted in substantial regeneration of forest, which now provides the villagers with fire wood, herbs, food and a wide variety of other non-timber forest products (*pers comm.* village elder: Mr. Chang Thoedpanit, informant on March 2015).

Forest inventory

Species names, D, and H were recorded for all woody plants with $D \geq 1$ cm in each plot. H was measured using a digital clinometer. Woody plant community composition was assessed using the Shannon–Wiener index, Shannon–Wiener evenness, species richness, ecological importance value index (IVI) and Sorensen’s similarity index. Vernacular names of all species were provided by a local guide, with many years of experience, working alongside a professional botanist, and subsequently translated into scientific names, using A Field Guide to Forest Trees of Northern Thailand (Gardner et al. 2000). Identifications were cross-checked with specimens in the Herbarium of Department of Biology, Faculty of Science, Chiang Mai University (CMUB). All plant names are accepted names confirmed by using The Plant List (<http://www.theplantlist.org>). Moreover, the classification of pioneer and climax species were based on Maxwell and Elliott (2001), Sinhaseni (2008), and Vaidhayakarn and Maxwell (2010).

Sampling design and harvesting

Three different criteria were used to select trees for harvesting. Firstly, three individual trees of each of the tree species that cumulatively comprised 50 percent of total IVI were selected in each diameter class sizes; (1) 1–10 cm, (2) 11–20 cm, (3) 21–30 cm, and (4) 31–40 cm, and felled in each study plot. Secondly, three of the tree species that were present in each study plot were randomly selected and felled. Thirdly, one tree of every species, previously designated as “framework species”—(i.e. those that foster ecosystem recovery due to high survival and growth rates, dense shady crowns and attractiveness to seed-dispersing animals

(Elliott et al. 2003)) was randomly selected and felled. The sample trees were felled from March 2015 to October 2016 and prepared for ABG determination, adapting the methods of Viriyabuncha (2003), Walker et al. (2012) and Picard et al. (2012), with permission from the Chiang Mai Provincial Office for Natural Resources and Environment.

After felling, stem diameter at the base (D_0) and breast height D (cm) and tree height H (m) were measured. Stem circumference was measured at 1-m intervals from the base to the first branch). Cross-cutting into 1 m logs started from the base (D_0) and continued to the top of tree stem, following the main stem. Any branches and leaves on the logs, including the last portion measuring less than 1 m, were removed and separated from the main logs. Logs were then labelled and the fresh weight of each log was recorded. Subsequently, every 1-m stem log was cross-cut at the base, to create 3–5 cm thick discs at 1-m intervals along the stem. Irregularly shaped trunks were excluded from this procedure, due to the difficulty of measuring their volume. The fresh weight of the discs was recorded, before measurements to calculate their volume (cm^3) (Walker et al. (2012) (Eq. 1):

$$Volume = \pi \times \left(\frac{D_1 + D_2}{2} \right)^2 \times \left(\frac{T_1 + T_2}{2} \right) \quad (1)$$

where *Volume* is volume of disc sample (cm^3), D_1 is first diameter of sample (cm), D_2 is second diameter of sample (cm), T_1 is first thickness of sample (cm), T_2 is second thickness of sample (cm) (Supplementary Table S1).

After recording the fresh weight of every branch, all branches in each class were mixed to draw a subsample of approximately 800 g for each diameter class. Similarly, all leaves were mixed to subsample approximately 800 g. The same method was used for coppiced trees by considering each coppice as an individual stem. All tree subsamples were then oven-dried in the laboratory to constant weight at 70 °C for leaf samples and at 105 °C for woody samples, according to Picard et al. (2012).

Tree discs were ground by sawing from the outside to the centre with a power jigsaw. The ground discs from each tree were mixed and weighed, to create three separate samples to allow for replication. Randomly chosen dried branches in different class sizes were ground, using the same method as discs. Finally, dried leaves were randomly chosen and pulverised with a blender. Three ground samples of these tree part were prepared. All ground samples were sent for carbon analysis separately, using an elemental analyser: LECO CHNS-932 and VTF-900 at the Scientific Equipment Center, Kasetsart University, Bangkok, Thailand. The carbon concentration of wood dry mass was analysed in 899 samples from 23 destructive tree species. Subsequently, average total carbon content of each tree was calculated across all tree parts.

Wood density was calculated using the disc samples. After measuring, drying and weighing the discs (as described above). Wood density measurement and calculation followed Chave (2006) and Donegan et al. (2014) (Eq. 2).

$$WD = \frac{m_{dry}}{V_{fresh}} \quad (2)$$

where *WD* is wood density (g cm^{-3}), m_{dry} is oven-dried mass (g), V_{fresh} is green volume (cm^3).

In addition, an increment borer (diameter = 5.15 mm) was used to collect core samples from every tree species in the 7Y and SF plots. However, this method could not be used for the smaller trees ($D < 4.5$ cm). For this reason, only the disc sample method was used in the 4Y plot.

Model development and selection

Allometric equations for trees usually take the form of a power relationship (Eq. 3) or logarithmically transformed power equations (Eq. 4) for predicting AGB (Chave et al. 2005):

$$Y = aX^b \quad (3)$$

$$\ln(Y) = \ln(a) + b\ln(X) \quad (4)$$

where Y is the dependent variable, usually dry biomass in kg, X is the independent variable, usually tree size and/or tree height, a is a constant or intercept, and b is the exponent or slope, \ln is natural logarithm. Ordinary least squares (OLS) regression is used to estimate a and b .

Data were transformed using natural logarithms for linear regression fitting methods (Eq. 4). First, models were developed with AGB (kg) as the dependent variable and D (cm) as the only independent variable. Next, H (m) or WD (g cm^3) variables were added to the function, individually and in combination, as in previously published models, i.e. D (Brown 1997; IPCC 2003), D^2H (Ogawa et al. 1965; Tsutsumi et al. 1983; Chave et al. 2005, 2014; Djomo et al. 2010) or $D^2H \times WD$ (Chave et al. 2005, 2014).

Mixed-species allometric models were developed and the best-fit model and variables were selected, based on the coefficients of determination (R^2), residual standard error of the estimate (RSE), average deviation ($S\%$) (Eq. 5) and akaike information criterion (AIC) (Chave et al. 2005). The best-fitting regression model was deemed to be the one with highest R^2 , lowest RSE, $S\%$ and AIC and fewest parameters (Basuki et al. 2009; Chave et al. 2005, 2014; Djomo et al. 2010; Huy et al. 2016a; Lin et al. 2017; Nam et al. 2016).

$$S\% = \frac{100}{n} \sum_{i=1}^n \frac{|\hat{y}_i - y_i|}{y_i} \quad (5)$$

where $S\%$ is the average deviation, \hat{y}_i is observed dry weight of tree i , y_i is the predicted dry weight of tree i , and n is number of observations).

Model validation and comparison

All data from the 136 destructive samples were randomly split 200 times into training data and validating data. Eighty percent of the observed data (109 trees) were used for model development, whilst 20% (27 trees) were used for model validation. Cross-validation statistics were computed for each iteration, and averaged over the 200 iterations. The models were validated and compared by validation of percent bias (Bias), root mean square percentage error (RMSE) and mean absolute percent error (MAPE). Positive or negative biasness indicated over- or under-estimation of AGB respectively (Eq. 6). RMSE (Eq. 7) (standard deviation of the residuals) measured how spread out the data were around the line of best fit. Finally, MAPE (Eq. 8) (average absolute percent error for each time period minus actual values divided by actual values) measured the percentage accuracy of the forecasts.

$$\text{Bias (\%)} = \frac{1}{R} \sum_{r=1}^R \frac{100}{n} \sum_{i=1}^n \frac{y_i - \hat{y}_i}{y_i} \quad (6)$$

$$\text{RMSE (\%)} = \frac{1}{R} \sum_{r=1}^R 100 \sqrt{\frac{1}{n} \sum_{i=1}^n \left(\frac{y_i - \hat{y}_i}{y_i} \right)^2} \quad (7)$$

$$\text{MAPE (\%)} = \frac{1}{R} \sum_{r=1}^R \frac{100}{n} \sum_{i=1}^n \frac{|y_i - \hat{y}_i|}{y_i} \quad (8)$$

where R is the number of iterations (200); n is the number of trees per iteration r and finally y_i and \hat{y}_i are observed and predicted biomass for the i th tree in each iteration. Smaller values indicate higher model validity.

After model selection, validation, and comparison, the final parameters of the selected models were fitted with the entire dataset (Huy et al. 2016b; Kralicek et al. 2017). All statistical analyses (regressions and tests) were performed using R, version 3.5.2 (R Core Team 2018). Finally, the data of 136 destructive samples was applied to the best selected equation as well as to other equations, to estimate the AGB_{pred} , and compare all the results with destructive AGB_{obs} from this study.

Results

Forest inventory

A total of 47 families, 86 genera and 118 species (including 1 bamboo species; *Gigantochloa albociliata*) were recorded. The numbers of tree species, trees and total basal area all increased with increasing fallow age; the highest being in the SF site. Shannon–Wiener and Shannon evenness indices indicated highest species diversity in the SF site and lowest in the 4Y plot. Both diversity indices increased with increasing fallow age. Percentage similarity (Sørensen’s index) between plots was higher between the 4Y and the 7Y plots than between both the 4Y and 7Y plots and SF (Table 1). The data for each tree species in every study site showed are presented in Supplementary Table S2.

Table 1 Vegetation characteristics of the study plots 4-year fallow (4Y), 7-year fallow (7Y) and Secondary forest (SF) (for trees of $D > 1$ cm)

Study plot	4Y	7Y	SF
Elevation (m)	1090	1120	1254
Species richness	43	44	80
No. of trees	470	678	692
All individual stems	1791	1045	776
Coppice	1321	367	84
Density (stems/ha)	4975	2903	2156
Basal area (m ² /ha)	4.05	10.99	24.94
Shannon–Wiener diversity	2.8	2.99	3.74
Shannon evenness	0.74	0.79	0.85
<i>Sørensen's index (%)</i>			
4Y	–	55	36
7Y		–	29
SF			–

Sampling design and trees felled

Seventy-eight trees were sampled (136 individual stems, including coppicing trees) of 23 species, 19 genera and 14 families. D ranged from 1.0 to 32.9 cm and H from 2.1 to 19.3 m (Table 2, Supplementary Table S3). Since, tree heights in dense forest could not be accurately measured, the relationship between D and H was determined from destructive data, within a range of D of 1–21.6 cm. Ln (D) was linearly related to ln(H), with the latter having approximately constant variance. Therefore, a simple linear regression was used, to predict ln(H) from ln(D), by the ordinary-least-squares method. The residual standard deviation was 0.2058 with $R^2 = 0.836$ (Fig. 1).

Model development and selection

Model validation statistics (%Bias, %RMSE and %MAPE), averaged over 200 iterations, are presented in Table 3. Model 7 was the most reliable, having lowest values of validation statistics and fewer parameters requiring estimation. Eight common allometric models were fitted with data from the 136 felled tree stems (including coppices), to establish relationships between measured AGB and D, H, and WD as predictor variables. Adjusted R^2

Table 2 Felled tree species in the three study plots: number of trees (T), number of coppices (C), total stem samples (trees and coppices), diameter at breast height (D) range in cm, height (H) in m

Species	Family	T	C	Total (T+C)	D (cm)	H (m)
<i>Albizia chinensis</i>	Leguminosae	1		1	21.6	19.3
<i>Aporosa villosa</i>	Phyllanthaceae	5	13	18	1.4–15.2	2.1–11.3
<i>Archidendron clypearia</i>	Leguminosae	1		1	5.9	5.9
<i>Canarium subulatum</i>	Burseraceae	6		6	2.7–30.9	3.8–15.1
<i>Castanopsis acuminatissima</i>	Fagaceae	2	2	4	5.1–11.1	4.1–7.3
<i>Castanopsis diversifolia</i>	Fagaceae	4		4	5.1–11.5	5.9–14.6
<i>Castanopsis tribuloides</i>	Fagaceae	4		4	4.8–15.3	6.5–16.5
<i>Dalbergia cultrata</i>	Leguminosae	4		4	5.2–10.8	5.0–8.9
<i>Eugenia fruticosa</i>	Myrtaceae	3	3	6	10.8–15.1	2.2–8.7
<i>Ficus fistulosa</i>	Moraceae	1	2	3	1.3–1.9	3.1–3.3
<i>Ficus semicordata</i>	Moraceae	1	1	2	2.1–3.3	3.9–4.0
<i>Helicia nilagirica</i>	Proteaceae	4		4	5.1–19.1	5.9–13.4
<i>Ilex umbellulata</i>	Aquifoliaceae	3	4	7	1–4.1	2.3–4.8
<i>Lithocarpus polystachyus</i>	Fagaceae	11	12	23	1–18.1	2.3–16.8
<i>Phoebe lanceolata</i>	Lauraceae	3		3	3.6–12.6	3.8–15.5
<i>Phyllanthus emblica</i>	Phyllanthaceae	5	14	19	1.8–13.1	3.3–10.7
<i>Quercus kingiana</i>	Fagaceae	7	1	8	6.9–32.9	4.9–13.6
<i>Quercus semiserrata</i>	Fagaceae	1		1	10.8	8.7
<i>Sapindus rarak</i>	Sapindaceae	1		1	16.2	15.5
<i>Sarcosperma arboreum</i>	Sapotaceae	1		1	6.1	7.2
<i>Schima wallichii</i>	Theaceae	4	4	8	2.2–17.8	3.9–17.0
<i>Styrax benzoides</i>	Styracaceae	3	1	4	4.1–10.5	5.3–8.2
<i>Wendlandia tinctoria</i>	Rubiaceae	3	1	4	1.4–8.5	2.8–11.7
Total		78	58	136	1–32.9	2.1–19.3

Fig. 1 Relationship between tree diameter (D) cm and tree height (H) m in natural log scale for trees with D ranging from 1 to 21.6 cm (n = 134)

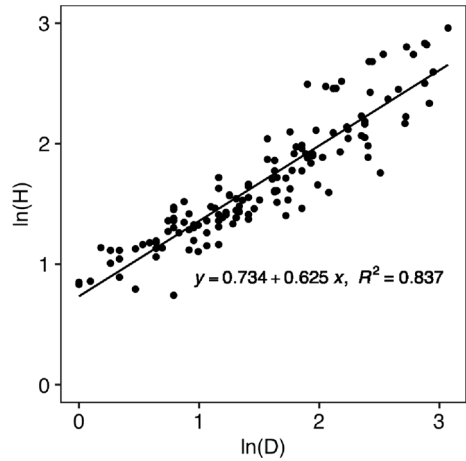


Table 3 Model validation and comparison among eight common models

Variable	Model	Equation formula	Bias (%)	RMSE (%)	MAPE (%)
D	1	$\ln(\text{AGB}) = a + b \ln(D)$	-6.66	37.22	29.33
	2	$\ln(\text{AGB}) = a + b \ln(D) + c (\ln(D))^2$	-6.19	38.30	28.27
D, H	3	$\ln(\text{AGB}) = a + b \ln(D) + c \ln(H)$	-6.27	35.29	26.24
D, WD	4	$\ln(\text{AGB}) = a + b \ln(D) + c \ln(\text{WD})$	-5.46	33.26	25.72
D ² H	5	$\ln(\text{AGB}) = a + b \ln(D^2H)$	-6.35	35.56	26.17
D ² H, WD	6	$\ln(\text{AGB}) = a + b \ln(D^2H) + c \ln(\text{WD})$	-4.91	29.88	22.16
	7	$\ln(\text{AGB}) = a + b \ln(D^2H \times \text{WD})$	-4.85	29.62	22.02
D, H, WD	8	$\ln(\text{AGB}) = a + b \ln(D) + c \ln(H) + d \ln(\text{WD})$	-4.89	29.83	22.30

Cross-validation statistics were computed for each iteration of randomly selected validation data, and averaged over the 200 iterations; N = 109

AGB = above-ground dry biomass (kg); D = stem diameter at breast height (cm); H = tree height (m); WD = wood density (g cm³). In model formulae, 'a', 'b', 'c', and 'd' are the coefficient values of the allometric regression models. Sources Model 1: Brown (1997), Model 2: IPCC (2003), Model 3: Basuki et al. (2009), Model 4–6: Djomo et al. (2010), Model 7, 8: Chave et al. (2005, 2014)

values exceeded 0.9 in all models. Including H or WD in the equations increased the goodness of fit (R²) slightly and model validity (RSE, AIC and %S all decreased). Model 7 was the most reliable, having the highest adjusted R², lowest RSE (0.298) and AIC (61.3) and low average S% (21.64).

Species-specific models were generated from data from > 10 felled trees of the 3 species that were dominant in all three sites: *Lithocarpus polystachyus* (n = 23, D: 1–18.1 cm), *Phyllanthus emblica* (n = 19, D: 1.8–13.1 cm) and *Aporosa villosa* (n = 18, D: 1.4–15.2 cm). For *Lithocarpus polystachyus*, Model 7 (D²H × WD) provided the most reliable prediction of AGB (R² = 0.99). However, for *Phyllanthus emblica* and *Aporosa villosa*, model 2, with D as the sole independent variable, resulted in the best fit, with highest adjusted R² and lowest RSE and AIC (Supplementary Table S4).

The species-specific models for *Lithocarpus polystachyus* showed the same trend as the mixed-species model did, with D²H × WD resulting in the best fit for AGB determination. All three species showed highly significant correlations between AGB and D, AGB and H,

and between D and H ($p < 0.001$). However, with *Lithocarpus polystachyus*, the correlations between D and WD and between H and WD ($p < 0.05$) were more highly significant, compared with the other two species, for which correlations with WD were not significant. Adding WD in Models 4, 6, and 8 did not result in any statistically significant correlations. Furthermore, using more parameters did not improve the accuracy of the models for *Phyllanthus emblica* and *Aporosa villosa* for AGB estimation, with the exception of Model 6 of *Phyllanthus emblica*. Even though WD improved the accuracy of Model 7 for *Phyllanthus emblica* and *Aporosa villosa*, lowest AIC values were obtained with Model 2, which used D as the sole independent variable.

Wood density

Wood density varied considerably ($0.23\text{--}0.75\text{ g cm}^{-3}$), averaging $0.52 \pm 0.09\text{ g cm}^{-3}$ (Supplementary Table S5). Biomass was estimated for all studied species (totally, 117), using average wood-density measured during our study for 79 species, data from the global wood density database (GWD) for 23 species (Zanne et al. 2009) and genus-level data for the remaining 15 species that were not included in the GWD. As expected, Duncan's Multiple Range tests revealed significant differences in mean WD between some species (when $n \geq 3$) ($p < 0.05$) (Fig. 2, Supplementary Table S6).

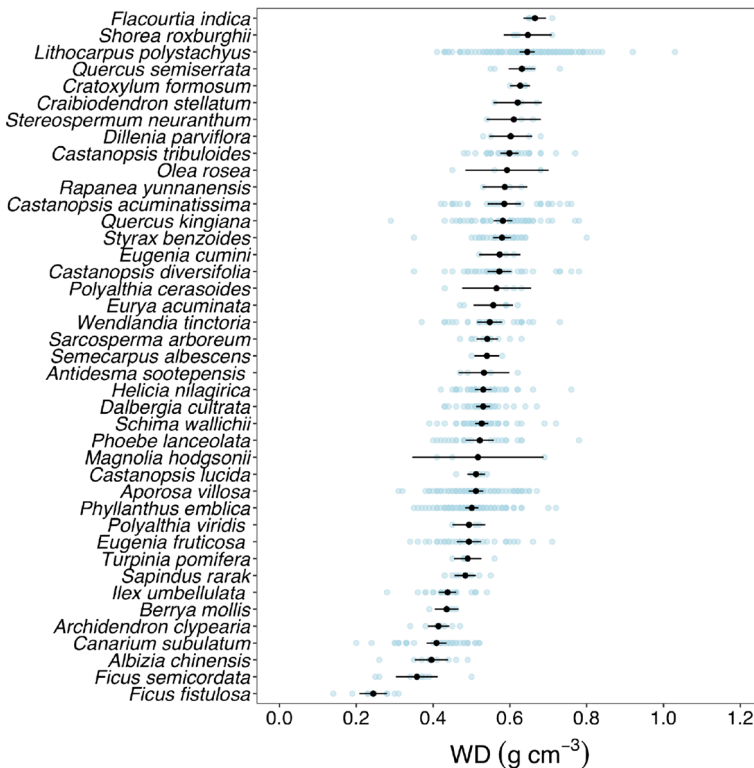


Fig. 2 Average wood density (WD in $\text{g cm}^{-3} \pm 95\%$ CI) of tree species ($n \geq 3$)

Carbon content

Differences in species-specific average carbon content were significant (Duncan’s Multiple Range test, $p < 0.05$). *Archidendron clypearia* wood had the highest carbon content (mean 46.73%, SD 2.08), whilst that of *Ficus fistulosa* had the lowest (mean 39.43%, SD 3.87). Averaged across all species, mean carbon content was 44.84% (SD 1.63) (Fig. 3, Supplementary Table S7).

Discussion

Developing allometric models

This study developed allometric equations, based on previously established models, starting with D as the sole variable, (Brown 1997; Hashimoto et al. 2004; Basuki et al. 2009; Kenzo et al. 2009) and subsequently incorporating H e.g. D^2H (Ogawa et al. 1965; Tsutsumi et al. 1983; Chan et al. 2013) and WD in various functions e.g. $D^2H \times WD$ (Chave et al. 2005, 2014). As expected, introducing more independent variables increased the reliability of the equations, as shown by increased R^2 and reduced values of AIC, RSE and S%. Chan et al. (2013) also reported that adding tree height into models (as D^2H) strengthens correlation with AGB. The AIC values of models, which included the D^2H function, were

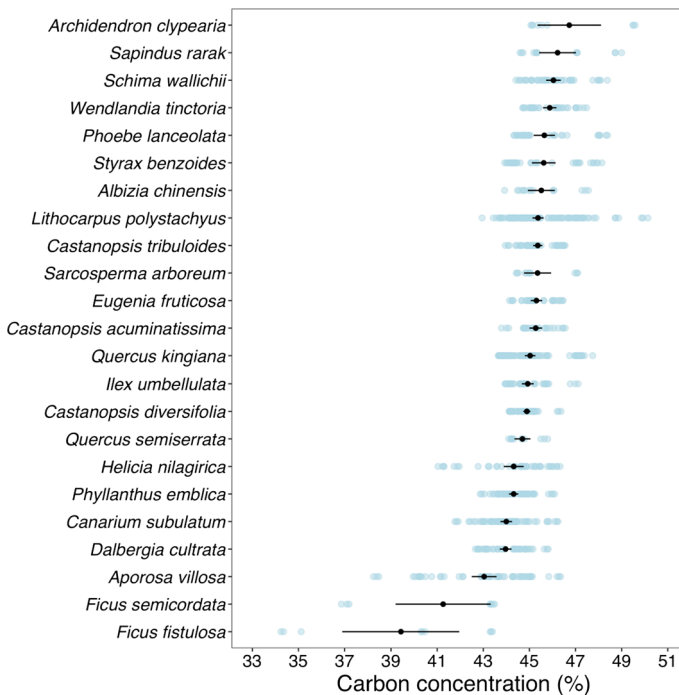


Fig. 3 Average carbon concentration (%) among felled tree species. Error bars represent the 95% confidence interval

lower than for models that used D and H separately. Combinations of all 3 variables (D, H, and WD) improved the goodness of fit, which was maximized in Model 7 ($D^2H \times WD$). Several other authors confirm that inclusion of WD improves the accuracy of allometric equations (Chave et al. 2005, 2014; Basuki et al. 2009; van Breugel et al. 2011; Chaturvedi and Raghubanshi 2013; Nam et al. 2016; Huy et al. 2016a; Kralicek et al. 2017).

Model comparison

Each model type was cross-validated and compared separately to models from previous studies, using the same number of independent variables (Supplementary Table S8). RMSE and MAPE for Model 1 (with D as the sole independent variable) were comparable with those reported by Kenzo et al. (2009). Most of the previously published models and Model 1 and 2 from this study resulted in a negative %Bias, the only exception being that of the Kenzo et al. (2009), which underestimates AGB. Nevertheless, RMSE and MAPE for Model 2 were higher than for Model 1. However, one D-based variable, developed in the present study, predicted considerably lower AGB, compared with the models of Brown (1997) and IPCC (2003). For the two-parameter Model 5 (D^2H), Bias, RMSE and MAPE values were similar to those reported by Chan et al. (2013) and McNicol et al. (2015), but much lower than those derived from Tsutsumi et al.'s (1983) model, even though the latter was based on data collected in Thailand. This might be attributed to Chan et al.'s (2013) and McNicol et al.'s (2015) use of similar D sizes to this study (1.2–25.4 and 1.7–36.2 cm, respectively), to establish their models, whereas Tsutsumi et al. (1983) based their model on much larger trees. Model 7, which combined all 3 variables ($D^2H \times WD$), resulted in lower Bias, RMSE, and MAPE values, compared with all three equations from Chave et al. (2005, 2014), which incorporated the same variables.

One of the 200 validation datasets was chosen from the lowest values of %Bias, %RMSE, %MAPE and applied to selected models from this study (Model 1, 2, 5, and 7) and other previous models for AGB estimation. AGB evaluated with all the models was termed “AGB_{pred}” and compared with “AGB_{obs}”—the observed collected AGB data in this study. AGB_{pred} values, from models based solely on D (Models 1 and 2 in this study), were broadly similar to previously published values (Brown (1997) (dry forests) and Kenzo et al. (2009)). Model 1 resulted in the best-fitted D-based equation, with a result close to that of Kenzo et al.'s (2009) model. This may be explained by the fact that these two models were developed from trees within approximately the same size range of D: 0.11–28.66 cm in Kenzo et al. (2009), compared with 1.0–32.9 cm in this study. In contrast, both the Brown (1997) model and the IPCC (2003) model for moist tropical forests overestimated AGB_{pred} and showed a higher % relative error. The Kenzo et al. (2009) model, on the other hand, underestimated the % relative error (Fig. 4). and showed a positive %Bias. Of the models using D^2H as explanatory parameters, Tsutsumi et al. (1983) and McNicol et al. (2015) overestimated AGB. However, Chan et al.'s (2013) model tended to under-predict biomass, even though it was built using data from similar tree sizes to our study (1.2–25.4 cm). Chan's model also underestimates AGB, when using the D^2H equation and explanatory data from their study and comparing the results with those of Tsutsumi et al.'s (1983) equation. Lastly, the model that included WD (as $D^2H \times WD$) resulted in the highest goodness-of-fit, compared with the other models tested in this study. The results clearly showed that all equations from pantropical forests over-predict AGB, compared with Model 7. Such overestimation has also been reported by McNicol et al. (2015) and van Breugel et al. (2011), when using Chave et al.'s (2005) moist-forest equation for biomass estimation

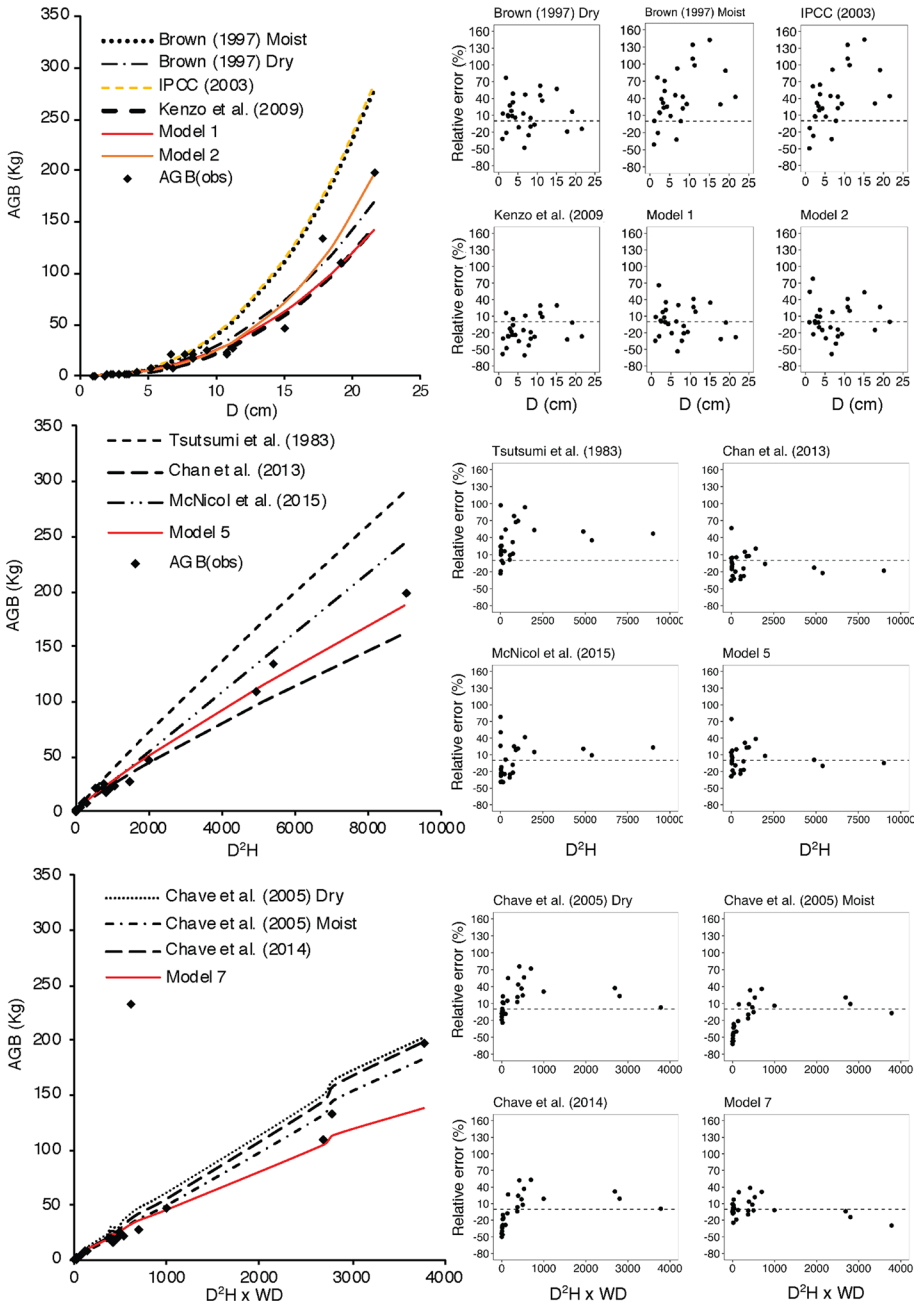


Fig. 4 Comparison of above-ground biomass from validation data (AGB_{obs}), and predicted values, using previous models and the best fit AGB model. Relative errors are shown in the right-hand panels for D , D^2H and $D^2H \times WD$ parameters

in secondary forests. The trend line from Chave et al.'s (2005) equation for dry forests resulted in higher over-prediction than did the other models. However, the new equation from Chave et al. (2014) resulted in lower values of % relative error.

Comparison of AGB estimation with other previous equations

D, H and WD data, from 136 destructive samples, were used to compare estimates of AGB_{pred} among all the models listed in Supplementary Table S8 and with observed AGB_{obs} from destructive sampling (Table 4). Inputting the field data from this study to both of the moist-tropical-forest equations (Brown 1997; IPCC 2003) resulted in high values of Bias, RMSE, and MAPE, and high overestimation of AGB (47% for Brown's 1997 moist model and 48% for the IPCC 2003 model). Similarly, Kenzo et al. (2009) reported overestimation of approximately 100%, when using secondary-forest data with Brown's (1997) moist-forest equation. However, when using Brown's (1997) dry-forest equation, AGB_{pred} did not deviate significantly from AGB_{obs} , probably because his equation was developed using a D range of 5–40 cm (similar to the range used in the present study). Moreover, van Breugel et al. (2011) suggested that models that focus on larger trees (Brown 1997; Chave et al. 2005) may overestimate the biomass of smaller trees.

Chan et al. (2013), Kenzo et al. (2009) and Model 7 from the present study all predicted lower AGB_{pred} , compared with the other equations. Although McNicol et al. (2015) developed their model in "moist" forest in Lao PDR, the estimation error for total biomass accumulation was relatively low, whilst the percent error in younger fallows was relatively high (4Y and 7Y) (Table 4). Furthermore, Tsutsumi et al.'s (1983) equation—commonly used in Thailand—overestimated AGB_{pred} by approximately 17%. However, using Chave et al.'s (2014) equation, AGB_{pred} was very similar to AGB_{obs} and it performed better than Chave et al.'s (2005) previous equation. This may be explained by use of a broader range of datasets (from both dry and moist forests, disturbed areas and secondary forests) to derive Chave et al.'s more recent equation. In contrast, Chave et al.'s (2005) earlier study used data from only 27 sites, only three of which were dry forest. In the youngest fallow site (4Y), the model developed in this study, as well as that of Chan et al. (2013), generated the best predictions, with the former showing a smaller error of estimation of overall biomass

Table 4 Error percentage (% error) of above-ground biomass estimation for the study plots and total error for each model

Variable	Source	% Error			
		4Y	7Y	SF	Total
D	Brown (1997) Dry	23	-12	-3	-6
	Brown (1997) Moist	41	40	54	47
	IPCC (2003)	36	41	55	48
D ² H	Kenzo et al. (2009)	-13	-27	-19	-22
	Tsutsumi et al. (1983)	23	-9	40	17
	Chan et al. (2013)	-9	-45	-18	-30
	McNicol et al. (2015)	-20	-29	11	-9
D ² H × WD	Chave et al. (2005) Dry	14	-11	21	6
	Chave et al. (2005) Moist	-31	-25	3	-11
	Chave et al. (2014)	-16	-17	14	-1
	Model 7 (This study)	9	-35	-13	-23

than the other models did. This result suggests that the model from the present study provided more precise AGB predications for smaller sized trees (1–7 cm) in 4Y than 7Y and SF sites. A likely explanation is that small trees (D:1–10 cm) accounted for 80% of those used to create the model.

Adding wood density, as an explanatory variable, resulted in a significantly better fit for the mixed-species model. Several previous studies recommended inclusion of WD for both local and global models, including models for tropical forests (Chave et al. 2005, 2014; van Breugel et al. 2011; Fayolle et al. 2013). However, it is important to note that average WD varies not only between species, but also among trees of the same species, and even within an individual tree, depending on tree age, successional guild, environment and geographical location (Chave 2006; Henry et al. 2010; Yeboah et al. 2014). Also, since average WD can vary significantly among different tropical regions, locally developed models may be less useful, if WD is not included (Baker et al. 2004; Chave et al. 2009; van Breugel et al. 2011). This may explain why Kenzo et al.'s (2009) model (in which WD averaged 0.35 g cm^{-3}) and Chan et al.'s (2013) model (in which WD averaged 0.38 g cm^{-3}) underestimated AGB, compared with the present study (in which WD averaged 0.52 g cm^{-3}).

AGB accumulation in fallows and secondary forests

Model 7 ($D^2H \times WD$) was used to estimate plot-level AGB, together with a bamboo-specific allometric equation (Yuen et al. 2017) to include the bamboo plants (*Gigantochloa albociliata*) that grew in the 7Y plot. In the 4Y plot, AGB amounted to 10.3 Mg ha^{-1} (including 4.6 Mg ha^{-1} carbon), of which remnant big trees accounted for 12.2%. This level of biomass accumulation was comparable with that recorded in a 1-year-fallow in East Kalimantan ($8\text{--}10 \text{ Mg ha}^{-1}$) (Hashimoto et al. 2004) and a 5-year-fallow in Myanmar (13.2 Mg ha^{-1}) (Chan et al. 2016). In contrast, active restoration appears to accumulate far more biomass over a similar period, compared with passive natural regeneration, on abandoned agricultural land in northern Thailand. In the upper Mae Sa Valley, at a similar elevation to that of the present study, Jantawong et al. (2017) reported biomass accumulation of 29.9 Mg ha^{-1} , 5 years after cessation of cultivation, followed by tree planting (by the framework species method Elliott et al. 2003)—almost treble that achieved by natural regeneration in the present study.

In the 7Y plot, the few older trees left standing increased AGB to 38.3 Mg ha^{-1} ($17.4 \text{ Mg C ha}^{-1}$)—far more than for fallows in Myanmar, aged 1–25 years ($3.7\text{--}31.8 \text{ Mg ha}^{-1}$) (Chan et al. 2016). Estimated AGB in the SF plot was 105.3 Mg ha^{-1} ($47.7 \text{ Mg C ha}^{-1}$) (approximately 50 years since cessation of shifting cultivation), even though signs of ongoing human disturbance were observed. It is interesting to note that Jantawong et al. (2017) reported a similar level of AGB accumulation (100.8 Mg ha^{-1}) just ten years after tree-planting by the framework species method, under similar conditions to those of the present study, whilst 14-year-old actively restored plots reportedly achieved considerably higher amounts of biomass (240.5 Mg ha^{-1}), greatly exceeding those of approx. 50-year-old disturbed SF, recorded in the present study. This suggests that complementing the management of natural regeneration with tree planting could substantially increase biomass accumulation and carbon sequestration on fallow land. Such evidence contributes to the ongoing debate over the relative merits of active versus passive restoration techniques (Reid et al. 2018; Atkinson and Bonser 2020).

AGB increased with fallow age (see also Fukushima et al. 2008; Chan et al. 2013; Mukul et al. 2016; Borah et al. 2018; Jha et al. 2020). Secondary forests are important

carbon sinks throughout the tropics, yet there have been few studies of them. More detailed carbon assessments are needed, because many factors affect carbon accumulation, such as tree species, forest type, forest structure, stand age, geographical factors (slope, aspect, and altitude), soil fertility, prevailing climate, land use history and land management (Chan et al. 2013; Yeboah et al. 2014; Chanthorn et al. 2017).

Carbon content

Species-specific carbon content varied considerably (see also Thomas and Malczewski 2007; Zhang et al. 2009; Martin and Thomas 2011). Average carbon content, across all tree species in this study, was $44.84\% \pm 1.63$. This is considerably lower than the 50% value that is most commonly used to convert biomass to carbon stock in carbon stock assessments (Brown 1997). It is also slightly lower than 47%, which the IPCC (2006) recommends for tropical forests, and the 48.97% recommended for seasonal evergreen forest in Thailand (Tsutsumi et al. 1983). However, the average carbon content in the present study is close to $44.67\% \pm 0.54$, which Jantawong et al. (2017) reported in a study of active restoration of seasonally dry upland evergreen forest, also in northern Thailand. If a carbon factor of 50% were to be applied to the data from this study, an overestimation of approximately 11.5% would result. This overestimation would decrease to 4.8% if a carbon factor of 0.47 were applied. Similarly, in Panamanian forests and tropical lowland Dipterocarp rainforest in Malaysian Borneo, overestimates of 5.3% and 6% respectively were reported, when a carbon factor of 50% was applied (Martin and Thomas 2011; Saner et al. 2012 respectively). This indicates that carbon content varies not only among species, but also among different forest types. Applying species-specific carbon content, or at least forest type specific values, is highly recommended for more precise carbon stock assessments. More studies of species- and site-specific carbon content would therefore be beneficial.

Biomass and carbon in the small trees ($D < 4.5$ cm)

More than half of all trees in the 7Y and SF sites had a D of < 4.5 cm (58 and 55% respectively). The 4Y plot had an even higher proportion of small trees 89%, accounting for 59% of the basal area. Accordingly, small trees contained 54% of the AGB and carbon in the youngest 4Y plot, whilst they accounted for 7% and 1% in the 7Y and SF plots respectively; a result in agreement with the findings of Chidumayo (2002) (reported by Chave et al. 2014). In short, large trees stored most carbon in older plots, whilst small trees stored most in younger plots. Consequently, surveys of young fallows (up to 4 years old) that do not include small stems (D : 1–4.5 cm) would underestimate ABG/ABC by around 50% or more. Therefore, it is essential that surveys include small trees, particularly in young regenerating forests.

Conclusions

This study established reliable allometric equations to predict AGB, in mixed-species fallows and secondary forests, by combining three explanatory variables: D , H , and WD ($D^2H \times WD$). Species-specific models were also developed. The best fitted model for *Lithocarpus polystachyus* used all three variables, whilst those for *Phyllanthus emblica*, and *Aporosa villosa* required only D as the sole independent variable. The allometric

equations, derived from the present study for small trees ($D < 4.5$ cm) (which are rarely considered in such studies), estimated biomass more reliably than previous studies in regenerating secondary forests and fallows—a forest condition found commonly throughout northern Thailand.

This study confirmed that carbon accumulation accelerates considerably as fallows age and that active restoration (e.g. tree planting and care) could further accelerate it. It also raises the possibility of using carbon value as an attractive economic incentive to promote forest conservation. For example, using the improved allometric equations from this study, carbon accumulation in fallows from Y4 to Y7 ($4.6\text{--}17.4$ Mg C ha⁻¹, over 3 years) averaged 4.27 Mg C ha⁻¹ yr⁻¹ (equivalent to 15.67 t CO₂ ha⁻¹ yr⁻¹). Applying the European Allowance Unit (EAU) market price at time of writing (26.93 EUR per tonne of CO₂, 30/09/20, <https://ember-climate.org/data/>) (since Thailand has no carbon market), yields an average carbon value of approximately 422 EUR ha⁻¹ yr⁻¹. In contrast, in Ban Ho village, average annual income from maize cultivation (one of the main drivers of deforestation in northern Thailand) is only about 180 EUR ha⁻¹ yr⁻¹ (based on an interview with the villager Mr. Somchai Thoedpanit, 28 November 2019). Even allowing for transaction costs, monitoring and evaluation costs and interest payments on start-up loans, it is highly likely that forest restoration and conservation could yield a higher income for villagers than their current mainstay—maize cultivation. Please also note that the above rough calculation only takes into account above-ground carbon. Inclusion of increases in below-ground carbon would add considerably to potential total carbon value.

The carbon measurement procedures, developed by this study, may be used in forest restoration and forest conservation projects, to ensure that stakeholders are fairly rewarded for their efforts, when REDD+ is finally implemented in Thailand, based on meaningful payments that reflect accurately the quantities of carbon sequestered, whilst also yielding a wide variety of other benefits from increased supplies of forest products to watershed services and opportunities to develop ecotourism.

Supplementary Information The online version contains supplementary material available at (<https://doi.org/10.1007/s11056-021-09844-3>).

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