LETTER • OPEN ACCESS

Mixed-species allometric equations and estimation of aboveground biomass and carbon stocks in restoring degraded landscape in northern Ethiopia

To cite this article: Mulugeta Mokria et al 2018 Environ. Res. Lett. 13 024022

View the article online for updates and enhancements.
Mixed-species allometric equations and estimation of aboveground biomass and carbon stocks in restoring degraded landscape in northern Ethiopia

Mulugeta Mokria¹,²,⁶, Wolde Mekuria³, Aster Gebrekirstos², Ermias Aynekulu¹, Beyene Belay⁴, Tadesse Gashaw⁵ and Achim Bräuning¹

¹ Institute of Geography, Friedrich-Alexander-University Erlangen-Nuremberg, Wetterkreuz 15, 91058 Erlangen, Germany
² World Agroforestry Centre (ICRAF), United Nations Avenue, PO Box 30677-00100, Nairobi, Kenya
³ International Water Management Institute (IWMI), PO Box 5689, Addis Ababa, Ethiopia
⁴ Amhara Regional Agricultural Research Institute, Bahir Dar, Ethiopia
⁵ International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Addis Ababa, Ethiopia
⁶ Author to whom any correspondence should be addressed.

Abstract

Accurate biomass estimation is critical to quantify the changes in biomass and carbon stocks following the restoration of degraded landscapes. However, there is lack of site-specific allometric equations for the estimation of aboveground biomass (AGB), which consequently limits our understanding of the contributions of restoration efforts in mitigating climate change. This study was conducted in northwestern Ethiopia to develop a multi-species allometric equation and investigate the spatial and temporal variation of C-stocks following the restoration of degraded landscapes. We harvested and weighed 84 trees from eleven dominant species from six grazing exclosures and adjacent communal grazing land. We observed that AGB correlates significantly with diameter at stump height $D_{30}$ ($R^2 = 0.78; P < 0.01$), and tree height $H$ ($R^2 = 0.41, P < 0.05$). Our best model, which includes $D_{30}$ and $H$ as predictors explained 82% of the variations in AGB. This model produced the lowest bias with narrow ranges of errors across different diameter classes. Estimated C-stock showed a significant positive correlation with stem density ($R^2 = 0.80, P < 0.01$) and basal area ($R^2 = 0.84, P < 0.01$). At the watershed level, the mean C-stock was 3.8 ($±0.5$) Mg C ha$^{-1}$. Plot-level C-stocks varied between 0.1 and 13.7 Mg C ha$^{-1}$. Estimated C-stocks in three- and seven-year-old exclosures exceeded estimated C-stock in the communal grazing land by 50%. The species that contribute most to C-stocks were Leucaena sp. (28%), Calpurnia aurea (21%), Euclera racemosa (20.9%), and Dodonaea angustifolia (15.8%). The equations developed in this study allow monitoring changes in C-stocks and C-sequestration following the implementation of restoration practices in northern Ethiopia over space and time. The estimated C-stocks can be used as a reference against which future changes in C-stocks can be compared.

1. Introduction

Tropical forests play a major role in regulating the earth’s climate through sequestering atmospheric CO$_2$ [1, 2]. However, tropical forests have become the second largest atmospheric source of CO$_2$ due to increased deforestation, large-scale land-use changes, and global climate change induced tree mortality [3–5]. Forest degradation is severe in Sub-Saharan Africa (SSA) [6–8] and is amplifying climate change-related risks such as drought and flooding in the region [9, 10]. Partly in response to these threats, significant attention has been paid to the consequences of tropical forest degradation on regional and global scales in recent years [11, 12]. Most notably, this attention has led to the establishment of an international policy...
framework, increased collaboration between states, and global initiatives to reduce deforestation and promote the recovery of degraded landscapes [13, 14]. In this line, the African Forest Landscape Restoration Initiatives (AFR100) targeted to restore 100 million hectares of degraded landscapes by 2030 in order to boost food security, sustain ecosystem benefit of trees, and improve the resilience of local communities towards the impacts of global climate change [15, www.afr100.org].

Ethiopia has been implementing extensive watershed management measures since the 1980s and has restored several degraded areas [16]. However, the contribution of these restored areas to mitigate climate change through carbon sequestration is not well understood. This gap partly stems from lack of biomass estimation methods, which are required to investigate the temporal and spatial changes in C-stocks following the implementation of restoration measures. Such information gap potentially affects collaboration between states and transnational organizations, as well as future efforts to increase the geographical coverage of restored landscapes [12, 17].

Generalized biomass equations have been used to estimate tropical forest carbon dynamics, and have played a significant role in improving data availability [18, 19]. However, the accuracy of aboveground biomass (AGB) estimation still falls behind what is required, especially in SSA [20, 21]. The main reasons for persistent inaccuracy were lack of site-specific biomass estimation models which can represent the heterogeneity of the study population in terms of species composition and tree-size variation [21–24]. To date, there is no mixed-species allometric model for small-size trees in SSA, including Ethiopia, leading to a high level of uncertainty in estimated AGB in the region. Thus, it is urgent and timely to develop site-specific allometric equations for mixed-species forest stands and to investigate carbon dynamics in restoring landscapes. The present study was conducted to derive various mixed-species allometric equations for small-sized trees and to identify the best allometric equation for the restoring landscape. We then applied the best equation to estimate AGB and compared the distribution of C-stocks in grazing exclosures and adjacent communal grazing land (CGL) to understand the importance of grazing exclosures in recovering the C-sequestration potential of degraded landscape in northern Ethiopia.

2. Materials and methods

2.1. Study area and climate characteristics

The study was conducted in ‘Gomit watershed’, located in South Gondar administrative zone, in the upper Blue Nile River catchment in northwestern Ethiopia (figure 1(a)). This watershed stretches to the east of Lake Tana and covers an area of 1483 ha (figure 1(c)). It contains six exclosures:\footnote{Exclosures are areas socially fenced from wood cutting, grazing by domestic animals and other agricultural activities with the goal of promoting natural regeneration of plants and rehabilitating formerly degraded communal grazing land [16].} Atikurit (ATK, 37.905°E, 12.116°N, age = 1 year); Markos (MAR, 37.897°E, 12.098°N, age = 2 years); Kikibe (KIK, 37.907°E, 12.103°N, age = 3 years); Enkurofaj (ENK, 37.894°E, 12.115°N, age = 4 years); Tinkish (TIN, 37.896°E, 12.121°N age = 5 years), and Deldali (DEL, 37.899°E, 12.101°N, age = 7 years). The exclosures are located close to the communal grazing land (hereafter, CGL, 37.898°E, 12.110°N) (SI appendix, figure S1 available at stacks.iop.org/ERL/13/024022/mmedia). We assume that before establishment, exclosures and the communal grazing land were in similar condition, because the exclosures were established on the same type of communal grazing land used for livestock grazing.

In the study watershed, major land use types include cultivated lands (23% of the land area), degraded secondary forest lands (53%), communal grazing land (18%), and other uses (6%) [25]. In the highlands of Ethiopia, including the upper Blue Nile Basin, the cattle population represents more than 75% of livestock population [26]. According to the Global Livestock Production and Health Atlas, the Amhara region cattle population density ranges from 64.7–93.8 (heads km\(^{-2}\)) (http://kids.fao.org/glpha/#). In this line, livestock population in the upper Blue Nile Basin is one of the main land-use change drivers and shows increasing trends of 1.5% per year [26, 27]. In the Ethiopian highlands, livestock pressure also affects the hydrological system and exacerbates water-related problems [28].

The study watershed is mountainous and characterized by a monsoonal unimodal rainfall pattern [29]. The rainy season occurs from June to September and accounts for 80% of the total annual rainfall. Based on data from the National Meteorological Agency of Ethiopia, the catchment received a mean annual rainfall of 1109.7 (±164.5 SD) mm over the period 1952–2014 (figure 1(b)). Monthly mean maximum and minimum temperatures ranged from 22.6°C–28.8°C and from 11.2°C–15.4°C, respectively.

2.2. Vegetation inventory

A vegetation survey was conducted on six exclosures and adjacent CGL located in the study watershed. In each exclosure and CGL, three transects were established perpendicular to the main slope of the terrain. To consider topographic variations, each transect was further divided into three landscape positions, namely foot slope (FS), mid (MS) and upper (US) slopes. Then, sampling plots of 20 m × 20 m size were established in each landscape position along with each transect. In total, 61 sample plots, ~21 in each of the three landscape positions were established across the study
watershed. Tree species encountered in each plot and their stem diameter ($D_{30}$) at 30 cm above the ground and total tree height ($H$, m) were recorded using a caliper and measuring tape, respectively. Since small-size trees dominate the area, we opted to measure the diameter at 30 cm above the ground [30, 31].

2.3. Tree harvesting and determination of aboveground biomass
To determine AGB and C-stocks, we first identified eleven dominant woody species using our vegetation inventory data following the approach used in [32]. To determine total AGB, we collected two to seven representative tree species from each study site. After measuring $D_{30}$ and $H$, the total aboveground components of the trees were harvested. The felled tree individuals were separated into the stem, twig, and foliage components. The fresh AGB of each component was weighed on the site using a spring balance ($\pm 0.01$ kg) [33]. To determine the dry matter contents of the sampled trees, representative sub-samples were collected randomly from each component of the tree.
Then, the sub-samples were weighed in the field, sealed in plastic bags, and transported to Adet Agricultural Research Center to determine their moisture contents. Samples were then oven-dried at 65 °C until constant weight was attained. The total oven-dried samples were weighed and the fresh-to-oven-dry weight ratios calculated. These ratios were used to convert the total fresh weights of sample trees measured in the field into total oven-dry weights [33, 34]. The carbon content in the AGB was estimated by multiplying the values of AGB by the default IPCC carbon fraction value of 0.47 [35].

2.4. Biomass model development and cross-validation test

Biomass estimation models were developed using non-linear regression equations based on either stump diameter ($D_{30}$) alone or in combination with their total tree height ($H$) as independent variables [33, 34]. Model cross-validation was conducted following a split-sample approach [36, 37] by randomly dividing the 84 sample trees into two equal parts. (Both halves of the dataset were used as a ‘training data set’ for model calibration (hereafter, F1/2D and S1/2D, $n = 42$ each), and as a ‘test data set’ for model validation (hereafter, CVD_F1/2D and CVD_S1/2D, $n = 42$ each). Finally, the full dataset (FD, $n = 84$) was used to build the final biomass estimation models. Model performance was checked using various goodness-of-fit statistics, such as coefficient of determination ($R^2$), standard error of estimate (SEE), index of agreement ($D$), mean absolute bias (MAB), percent bias (PBIAS), root mean square error (RMSE), prediction residuals sum of squares (PRESS), percent relative standard error (PRSE) and weighed Akaike information criterion ($AIC_w$) [29, 33, 38]. We also performed outlier and influence diagnostic test statistics, including Cook’s distance and Leverage point [39] (SI appendix: Materials and Methods). We compared the performance of our best model with seven previously published biomass estimation models from Ethiopia and elsewhere in the tropics. Finally, we used our best model to convert forest inventory data to AGB and C-stocks in the enclosures and CGL.

2.5. Statistical analysis

Pearson correlation tests were conducted to identify which plant biometric variables ($D_{30}$ or $H$) were most strongly correlated with measured total AGB of harvested trees. A correlation analysis was conducted between independent variables ($D_{30}$ and $H$). Pearson’s correlations were computed between estimated C-stock, stem density and basal area for each enclosure and CGL, as well as for different landscape positions, and at the watershed level. The differences among enclosures and communal grazing land and between plots at different landscape positions (FS, MS, US) in aboveground biomass and C-stock were assessed using one-way analysis of variance. The significance of differences between enclosures and CGL in mean AGB and C-stock was tested using the least significant difference test (LSD) with $p < 0.05$.

3. Results

3.1. Harvested tree species and their dendrometric relationship

The harvested dominant tree species, their dendrometric information ($D_{30}$, $H$) and the range of oven-dry biomass per plant species are presented in (SI appendix, table S1). The $D_{30}$, $H$ and measured AGB of the harvested trees ranged from 2.0–10.1 cm, 1.3–5.0 m, and 0.6–20.6 kg tree$^{-1}$, respectively. The correlations between AGB-D30 and AGB-H were significantly positive ($P < 0.01$) (figures 2(a) and (b)). We found only a weak correlation between $H$ and $D_{30}$ (figure 2(c)). Similarly, $H$-$D_{30}$ correlations were weak for non-harvested trees measured across all sites ($R^2 = 0.27$, $P < 0.01$) and varied between sites and across diameter classes for trees from the same site (SI appendix, figure S2).

3.2. Development and validation of a aboveground biomass estimation models

Models developed for predicting AGB and their performances are presented in table 1. In all model forms, the influence of coefficients was significant ($P < 0.001$). Model performance analysis (table 1) and further cross-validation test results (SI appendix, table S2) showed that Y8 is the best model, given the set of eight candidate models with an $AIC_w$ of 60%. The cross-validation test showed that model estimates were stable for the two ‘test datasets’ (F1/2D and S1/2D) (figures 3(a) and (b)). The parameter estimates for the coefficients $a$ and $b$ for model Y8 using F1/2D and S1/2D dataset showed negligible differences from those parameter estimates using the full dataset (FD, $n = 84$) (SI appendix, table S3). The PRSE, the regression, and influence diagnostic analysis further confirmed that parameter estimates were stable and reliable for model Y8 (SI appendix, figure S3). The biomass of the cross-validation dataset ($n = 42$, CVD_F1/2D or CV_S1/2D) estimated by model Y8 using F1/2D or S1/2D training dataset, showed negligible differences compared to biomass estimated using the ‘full dataset’ (FD) (figures 3(a) and (b)). The deviations of estimated averages from observed average AGB per tree, were $-4.8\% [-2.58\%]$ and $+4.3\% [+2.3\%]$ when using the ‘training’ dataset F1/2D [FD] and S1/2D [FD] equations, respectively (figures 3(a) and (b)).

3.3. Comparison of aboveground biomass equations with previously published equations

Model Y8 produced the lowest average relative error (PBIAS %) compared to the error produced using previously published equations (figures 4(a)–(h)). The equations used by Negash [33] and Ali [40] underestimated the total AGB by 18.6% and 70.3%, while the equation used by Ketterings [41], Kuyah [34],
Figure 2. Aboveground biomass of harvested trees as a function of diameter at stump height ($D_{30}$) (a), total tree height (b), and regression of tree height as a function of diameter at stump height ($D_{30}$) (c).

Figure 3. Relationships between estimated and measured total aboveground biomass of the cross-validations ‘test’ dataset. In figure (a) and (b), circles are the biomass estimates using the full dataset (FD, $n = 84$) equation, the crosses are the estimates calculated using the model developed by the first halves of ‘training’ dataset (F1/2D) and second halves of ‘training’ dataset (S1/2D), $n = 42$ each. The 1:1 lines indicate the cross-validation data (CVD), CVD_S1/2D (a) and CVD_F1/2D (b). The $R^2$ values in figures 3(a) and (b) show the relationships between estimated AGB using the half and the full data set, respectively.

Brown [42], Mugasha [43] and Zewdie [44] overestimated total AGB by 6.4%, 17.2%, 33.4%, 34.6%, and 94.3%, respectively (figures 4(b)–(h)). More importantly, the spread of error in estimated AGB was stable across different diameter classes in Y8, ranging from $-5.2\%$ to $8.7\%$, however, it was considerably higher in previously published biomass estimation models (SI appendix, figure S4).

3.4. Estimated aboveground biomass and carbon stocks in restoring landscape

Table 2 shows a summary of forest inventory results and estimated biomass and carbon stocks. Stem density, basal area (BA) and tree-size ($D_{30}, H$) varied between sites and plots across landscape positions (table 2). Tree size-class distribution profiles revealed that the diameter-class ranging from 3–6 cm constituted about 97% of the total population. They also contributed the largest proportion of basal area (BA) and total aboveground C-stocks (figures 5(a)–(c)). Large-diameter trees ($D_{30} > 9$ cm) were also scarce in the CGL and accounted for only 10%, they, however, stocked approximately 80% of the total estimated C-stocks in the CGL (figure 5(c)).

Estimated C-stock showed a significant positive correlation with stem density ($R^2 = 0.80, P < 0.01$)
Table 1. Equations and goodness-of-fit performance statistics for estimating biomass (kg dry matter/plant) of multiple tree species grown in the exclosures and communal grazing land across the upper Blue Nile River Catchment.

| Models | Coefficient | Performance statistics | PRSE | Rank |
|--------|-------------|-------------------------|------|------|
|        | a           | b                       | c    |      |
|        |             | R²                      | SEE  | MAB  |
|        |             |                         | PBIAS%| PRESS| RMSE |
|        |             |                         | AIC  | rAIC | AICw |
|        |             |                         |      |      |      |
| Y1 = a*(D30b) | 0.2655*** | 1.7737*** | 0.78  | 1.88  | 1.36 | 0.78  | 1.88  | 1.36 |
| Y2 = a*(D30b)² | 0.1681*** | –                      | 0.78  | 1.92  | 1.35 | –6.86 | 329.06 | 1.90  | 0.94  | 112.21 | 14.23 | 0.0  | 3.8   | 5     |
| Y3 = a*(D30b)²*(H)c | 0.2430*** | 1.5041*** | 0.5511*** | 0.82  | 1.73  | 1.27 | –0.16 | 279.99 | 1.70  | 0.95  | 98.80  | 0.82  | 0.4  | 19.5  | 7.8  | 25.0  |
| Y4 = a*(D30b)²*(H)b | 0.1257*** | 0.2539*** | –        | 0.78  | 1.88  | 1.32 | –9.73 | 323.31 | 1.85  | 0.94  | 111.67 | 13.69 | 0.0  | 14.4  | 46.2 |
| Y5 = a*(D30b)*(H)² | 0.1282*** | 0.886*** | –        | 0.66  | 2.34  | 1.61 | –12.98 | 494.98 | 2.31  | 0.91  | 148.88 | 50.90 | 0.0  | 26.3  | 14.6 |
| Y6 = a*(D30b+H)² | 0.0115*** | –                      | 0.47  | 2.90  | 2.18 | –41.73 | 796.90 | 2.88  | 0.88  | 183.95 | 85.97 | 0.0  | 6.1   | 0    |
| Y7 = a*(D30b+H)b | 0.2567*** | 1.1213*** | –        | 0.78  | 1.87  | 1.36 | –0.35 | 303.98 | 1.85  | 0.94  | 111.34 | 13.36 | 0.0  | 20.1  | 5.5  |
| Y8 = a*(D²30b+H)b | 0.2451*** | 0.7018*** | –        | 0.82  | 1.73  | 1.28 | 0.01  | 267.29 | 1.71  | 0.95  | 97.98  | 0.00  | 0.6  | 19.2  | 5.2  |

SEE, Bias, MAB are in kg per plant, n = 84. Y, D30, H, are aboveground biomass (kg/plant), diameter at stump height (30 cm) and total tree height (m), respectively. *** is significant at P < 0.001. Bold PRSE values indicate unreliable parameter estimates. A positive and negative PBIAS (%) indicates over- and underestimation of AGB. Model performance ranking was performed based on goodness-of-fit statistics (this table) and outlier and influence diagnostic test statistics, (Cook’s distance and Leverage point) (SI appendix, figure S3).
and basal area ($R^2 = 0.84, P < 0.01$) (SI appendix, figures S5(a)–(f)). Estimated C-stocks varied between sites and plots across landscape positions within the same exclosures and CGL (table 2). Plots located at the FS position displayed higher values of estimated C-stocks in MAR, KIK and CGL. In contrast, plots at MS position showed higher values of C-stocks in ATK, ENK, TIN and DEL (table 2). Site wise, the estimated C-stock was higher in the 7 year old exclosure (DEL = 4.7 Mg C ha$^{-1}$), while the lowest was found in the CGL (2.12 Mg C ha$^{-1}$) (table 2, figure 5(d)). At the watershed level, estimated C-stocks at the FS and MS landscape positions were significantly higher than estimated C-stock at the upper slope positions (figure 5(e)). The most important species in terms of C-stocks were *Leucaena* sp. (28%), *Calpurnia aurea* (21%), *Euclea racemosa* (20.9%) and *Dodonaea angustifolia* (15.8%). Site wise, *Euclea racemosa* in ATK and DEL; *Calpurnia aurea* in MAR, *Leucaena* spp. in KIK and ENK; *Dodonaea angustifolia* in TIN exclosures and *Croton macrostachyus* in CGL, were the most important species in terms of C-stocks. Each of these species represented 57, 64, 45, 86, 67, 27, and 82% of total estimated C-stocks in respective exclosures and CGL, respectively (SI appendix, figure S6).

4. Discussion

4.1. Aboveground biomass and dendrometric relationship across grazing exclosures

The relationship between stem diameter and tree height varied considerably across sites, as well as between different diameter classes within the same site, suggesting that tree-size differences and micro-site conditions may influence the $H$-$D_{30}$ relationships in the studied site. This is in line with previous studies that reported tropical tree $H$-$D_{30}$ correlations considerably vary from region to region due to variations in forest type and structure, climate and environmental conditions [45]. Such differences may also influence the coefficient values of biomass estimation models, and thus have important implications for the estimation of biomass and the carbon storage potential of tropical forests [41, 46, 47]. The highest correlation between $D_{30}$ and AGB (figure 2(a)) indicates that stem
Table 2. Summary of forest inventory results and estimated aboveground biomass and carbon stocks in the exclosures and communal grazing land.

| SITE NAME | Site-code | Exclosures age | Landscape position | Stem density (Plot⁻¹) | Mean D₃₀ (cm) | Mean H (m) | BA (m² ha⁻¹) | AGB (Mg ha⁻¹) | C-stock (Mg ha⁻¹) |
|-----------|-----------|----------------|---------------------|----------------------|--------------|-----------|-------------|--------------|------------------|
| ATIKURI | ATK | 1 | FS_1 | 74 | 3.1 | 2.1 | 1.4 | 3.7 | 1.7 |
|          |          |                | FS_2 | 157 | 2.8 | 2.0 | 2.5 | 6.8 | 3.2 |
|          |          |                | FS_3 | 72 | 2.8 | 2.0 | 1.1 | 3.1 | 1.5 |
|          |          |                | MS_1 | 183 | 3.0 | 2.0 | 3.5 | 8.8 | 4.1 |
|          |          |                | MS_2 | 321 | 3.0 | 2.0 | 5.6 | 14.8 | 7.0 |
|          |          |                | MS_3 | 195 | 3.0 | 1.9 | 3.4 | 8.7 | 4.1 |
|          |          |                | US_1 | 97 | 2.9 | 2.1 | 1.6 | 4.5 | 2.1 |
|          |          |                | US_2 | 16 | 2.5 | 1.8 | 0.2 | 0.5 | 0.3 |
|          |          |                | Average | 139 | 2.9 | 2.0 | 2.4 | 6.4 | 3.0 |
| MARKOS | MAR | 2 | FS_1 | 62 | 3.7 | 2.4 | 1.9 | 4.7 | 2.2 |
|          |          |                | FS_2 | 450 | 3.1 | 2.5 | 8.8 | 26.6 | 12.5 |
|          |          |                | FS_3 | 27 | 3.3 | 2.4 | 0.6 | 1.7 | 0.8 |
|          |          |                | MS_1 | 134 | 3.6 | 2.4 | 3.6 | 9.3 | 4.4 |
|          |          |                | MS_2 | 37 | 2.6 | 2.2 | 0.5 | 1.5 | 0.7 |
|          |          |                | MS_3 | 75 | 3.5 | 2.3 | 1.9 | 5.0 | 2.4 |
|          |          |                | US_1 | 44 | 3.3 | 2.8 | 1.1 | 3.1 | 1.5 |
|          |          |                | US_2 | 14 | 2.5 | 2.2 | 0.2 | 0.5 | 0.3 |
|          |          |                | US_3 | 6 | 3.7 | 2.6 | 0.2 | 0.5 | 0.2 |
|          |          |                | Average | 94 | 3.3 | 2.4 | 2.1 | 5.9 | 2.8 |
| KIKIBE | KIK | 3 | FS_1 | 234 | 4.2 | 2.9 | 8.4 | 23.7 | 11.1 |
|          |          |                | FS_2 | 115 | 4.3 | 3.2 | 4.6 | 13.5 | 6.4 |
|          |          |                | FS_3 | 39 | 3.5 | 2.2 | 1.0 | 2.6 | 1.2 |
|          |          |                | MS_1 | 63 | 3.9 | 2.5 | 2.1 | 5.0 | 2.4 |
|          |          |                | MS_2 | 48 | 3.2 | 2.1 | 1.0 | 2.6 | 1.2 |
|          |          |                | MS_3 | 487 | 3.4 | 2.2 | 11.4 | 29.1 | 13.7 |
|          |          |                | US_1 | 90 | 3.9 | 2.9 | 2.9 | 8.3 | 3.9 |
|          |          |                | US_2 | 9 | 2.9 | 1.8 | 0.2 | 0.5 | 0.2 |
|          |          |                | US_3 | 6 | 3.7 | 2.6 | 0.2 | 0.5 | 0.2 |
|          |          |                | Average | 123 | 3.6 | 2.5 | 3.6 | 9.6 | 4.5 |
| ENKUROTEJI | ENK | 4 | FS_1 | 3 | 2.9 | 2.0 | 0.1 | 0.1 | 0.1 |
|          |          |                | FS_2 | 17 | 3.1 | 2.1 | 0.3 | 0.9 | 0.4 |
|          |          |                | FS_3 | 202 | 4.6 | 4.1 | 8.7 | 29.1 | 13.7 |
|          |          |                | MS_1 | 87 | 4.9 | 4.1 | 4.4 | 14.1 | 6.6 |
|          |          |                | MS_2 | 203 | 4.1 | 3.5 | 7.0 | 22.8 | 10.7 |
|          |          |                | MS_3 | 94 | 4.1 | 3.3 | 3.3 | 10.3 | 5.0 |
|          |          |                | US_1 | 59 | 3.5 | 2.8 | 1.6 | 4.5 | 2.1 |
|          |          |                | US_2 | 16 | 5.2 | 3.1 | 1.0 | 2.3 | 1.1 |
|          |          |                | US_3 | 33 | 3.9 | 2.4 | 1.2 | 3.0 | 1.4 |
|          |          |                | Average | 79 | 4.0 | 3.0 | 3.1 | 9.7 | 4.6 |
| TINKISH | TIN | 5 | FS_1 | 49 | 3.8 | 2.5 | 1.8 | 4.5 | 2.1 |
|          |          |                | FS_2 | 18 | 3.2 | 2.3 | 0.4 | 1.0 | 0.5 |
|          |          |                | FS_3 | 21 | 3.4 | 2.8 | 0.5 | 1.5 | 0.7 |
|          |          |                | MS_1 | 187 | 3.6 | 2.2 | 3.6 | 13.6 | 6.4 |
|          |          |                | MS_2 | 328 | 3.5 | 2.1 | 8.3 | 20.8 | 9.8 |
|          |          |                | MS_3 | 164 | 3.4 | 2.1 | 3.8 | 9.5 | 4.5 |
|          |          |                | US_1 | 210 | 3.6 | 2.1 | 5.6 | 13.4 | 6.3 |
|          |          |                | US_2 | 185 | 3.5 | 2.1 | 4.8 | 11.6 | 5.4 |
|          |          |                | US_3 | 183 | 3.5 | 2.0 | 4.5 | 10.7 | 5.0 |
|          |          |                | Average | 149 | 3.5 | 2.2 | 3.9 | 9.6 | 4.5 |
| DELDALIT | DEL | 7 | FS_1 | 104 | 3.6 | 2.5 | 3.7 | 8.5 | 4.0 |
|          |          |                | FS_2 | 423 | 3.4 | 2.3 | 10.1 | 26.9 | 12.6 |
|          |          |                | FS_3 | 52 | 3.9 | 2.7 | 1.9 | 4.7 | 2.2 |
|          |          |                | MS_1 | 259 | 3.5 | 3.3 | 6.4 | 21.8 | 10.3 |
|          |          |                | MS_2 | 184 | 3.1 | 2.2 | 3.5 | 9.5 | 4.5 |
|          |          |                | MS_3 | 182 | 3.2 | 2.3 | 3.9 | 10.7 | 5.0 |
|          |          |                | US_1 | 14 | 4.4 | 2.5 | 0.6 | 1.4 | 0.6 |
|          |          |                | US_2 | 27 | 3.6 | 2.6 | 0.8 | 2.1 | 1.0 |
|          |          |                | US_3 | 75 | 3.3 | 2.6 | 1.7 | 4.9 | 2.3 |
|          |          |                | Average | 147 | 3.6 | 2.6 | 3.6 | 10.1 | 4.7 |
Table 2. Continued.

| SITE NAME | Site-code | Exclosures age | Landscape position | Stem density (Plot$^{-1}$) | Mean $D_{50}$ (cm) | Mean $H$ (m) | BA (m$^2$ ha$^{-1}$) | AGB (Mg ha$^{-1}$) | C-stock (Mg ha$^{-1}$) |
|-----------|----------|----------------|-------------------|-----------------------------|------------------|-------------|-----------------|-----------------|------------------|
| FS_1      | 30       | 6.9            | 2.5               | 7.2                         | 11.4             | 5.4         |                 |                 |                  |
| FS_2      | 44       | 6.0            | 1.9               | 9.0                         | 7.0              | 3.3         |                 |                 |                  |
| FS_3      | 13       | 8.9            | 2.2               | 5.4                         | 3.4              | 1.6         |                 |                 |                  |
| MS_1      | 32       | 2.5            | 1.5               | 0.4                         | 1.0              | 0.5         |                 |                 |                  |
| MS_2      | 45       | 4.2            | 1.8               | 3.4                         | 6.1              | 2.9         |                 |                 |                  |
| US_1      | 27       | 4.7            | 1.5               | 3.8                         | 3.3              | 1.5         |                 |                 |                  |
| US_2      | 31       | 4.0            | 1.8               | 2.0                         | 3.0              | 1.4         |                 |                 |                  |
| US_3      | 28       | 2.5            | 1.6               | 0.4                         | 0.9              | 0.4         |                 |                 |                  |
| GRAZING_LAND | CGL | n/a          |                   |                             |                 |             |                 |                 |                  |
| MS_2      | 43       | 4.2            | 1.8               | 3.4                         | 6.1              | 2.9         |                 |                 |                  |
| US_1      | 27       | 4.7            | 1.5               | 3.8                         | 3.3              | 1.5         |                 |                 |                  |
| US_2      | 31       | 4.0            | 1.8               | 2.0                         | 3.0              | 1.4         |                 |                 |                  |
| US_3      | 28       | 2.5            | 1.6               | 0.4                         | 0.9              | 0.4         |                 |                 |                  |
| Average   | 31       | 5.0            | 1.9               | 4.0                         | 4.5              | 2.1         |                 |                 |                  |

Figure 5. Proportions of stem density (a), basal area (b), and C-stock (c) across diameter classes in study landscape. Estimated C-stocks variation between sites (d) and between landscape positions (e). The letter, ‘sn’ indicates a significant difference, whereas ‘a’ indicates no significant difference.
diameter is one of the main predictors of tree biomass in the studied grazing exclosures and CGL. To this line, similar conclusions were reported in previous studies [30, 33, 43, 48].

4.2. Multi-species biomass estimation models and their performances

The predictive performance of different models using the full dataset ranged from 47%–82%. This variation might be attributed to allometric differences and predictors included in the models [39]. Based on cross-validation and performance statistics test, model Y8 that included $D_{30}$ and $H$ as predictors are the best from the given set of model forms. It explained 82% of the variance in measured AGB and produced the lowest relative error (0.01%), implying that using $D_{30}$ and $H$ together as predictor may increase model robustness, as it can partially help to capture the effects of site-specific $H$-$D_{30}$ relationship on biomass allometric equations [47, 49]. Moreover, the performance of our best model to make an accurate prediction is not an artifact of overfitting, because the value of the RMSE in the cross-validation test is close to the standard error (SE) of the full dataset (table 1, appendix, table S2).

In addition, the parameter values in the regression equations and cross-validations were stable across subsets of the ‘test’ dataset for our best model. The PRSE, the regression and the influence diagnostic analysis provided evidence that the parameter estimates were reliable in model Y8. This further supports our argument that Y8 is robust and can reliably be used to estimate the AGB in restoring degraded landscape and CGL. Moreover, the dominant tree species that are used for model development also occur dominantly in the degraded dry Afromontane forest areas and grazing exclosures in the study region [8, 16, 32, 50–57], indicating that model Y8 is representative for larger areas of northern Ethiopia. The diameter-alone model (Y1) is the second-best model and explained 78% of the variation in measured AGB, with an associated error of 0.82%. This model also produced acceptable PRSE values ($PRSE < 25\%$), as well as outliers and influential points lower than 10% (table 1, SI appendix, figure S3). Hence, Y1 can be considered as a potential AGB estimation model for the study area and other similar regions when data for tree height are not available.

4.3. Model comparison and importance of site-specific allometric equation

Compared to other generalized biomass estimation models, our site-specific allometric equation produced the lowest estimation error for the study area. A stable spread of error produced across different diameter-classes indicated that Y8 is able to capture the heterogeneity of the studied tree population in terms of species composition and tree-size variation [45, 47]. Our result is in line with several studies, which have concluded that site-specific AGB estimation models are more robust and reliable to convert forest inventory data to AGB [41, 43]. Assessing forest C-stock is an integral part of understanding global climate change impacts in the tropics [19, 58]. Thus, our model could play a considerable role in reducing biomass estimation uncertainties, which resulted from the lack of allometric equations for small-size trees [48]. More importantly, in northern Ethiopia, the foundation trees species (i.e. Juniperus procera and Olea europaea) of the dry Afromontane forest areas failed to regenerate and other pioneer species are overtaking the open spaces [51, 54]. Most of these pioneer species are similar to those species used to develop our model, thus, our mixed-species model is crucial to calculate the contribution of understorey trees and shrubs to total C-stocks in degraded secondary Afromontane forests. It might also facilitate a paradigm-shifting towards restoring landscapes from the focus on values of remnant degraded secondary forests and woodlands alone.

Furthermore, our model can be used to illustrate the magnitude of possible uncertainties in biomass estimation associated with the omission of small diameter trees from tropical forest inventories and C-stock estimation [59]. For example, the magnitude of AGB underestimation when small-size trees are not considered in biomass estimation, accounted for nearly 30% [60], between 12 and 49% [59], 25 and 45% [61] of total forest AGB. This, in turn, signifies the importance of small-size trees in forest carbon storage [62]. Therefore, it is obvious that reliable biomass estimation might have considerable implications in allocations of funds among various priorities and application and attribution of international climate-change mitigation funds for restoration measures. It might as well assist to evaluate the attainments of globally and regionally recognized sustainability goals, such as the Sustainable Development Goals, particularly the land degradation neutrality target [63] and the African Forest Landscape Restoration Initiative achievements [15]. Therefore, our biomass estimation model produced for small-size trees is relevant to monitor temporal and spatial changes in C-stocks and to improve the accuracy of AGB estimations, specifically in the context of monitoring carbon dynamics in grazing exclosures and their potentials in providing ecosystem services like mitigating climate change through sequestering atmospheric CO$_2$ in northern Ethiopia.

4.4. Spatial and temporal variation in AGB and C-stocks across the study watershed

Tree-size, stem density, and basal area considerably varied along landscape positions within the same exclosures and CGL. The highest AGB values were recorded in the plots located in foot slope and mid-slope...
positions. This might be attributed to the mass translocation from upper to lower landscape positions (e.g., soil, water, and organic materials such as leaves and branches), which create a favorable microclimate and nutrient input in lower topographic positions [47, 64, 65]. The high number of small-size trees in the study sites points towards a positive impact of exclosures to recover degraded landscapes [66, 67]. The magnitude of C-stock variation was considerably higher between plots in the same exclosures and CGL than between sites, indicating that micro-site conditions and landscape position play a significant role in forest C-stock dynamics [68, 69]. This further stresses that carbon pool investigations across different landscape positions are crucial for accurate estimations of C-stock on watershed levels and that they are needed to understand C-fluxes after the implementation of restoration practices. More importantly, together with remote sensing data, the estimated hectare-level C-stock might provide a great opportunity to monitor the dynamics of AGB and C-stock in restoring landscapes at a regional- or national-scale [70].

The significant positive relationships between estimated C-stocks, stem density and basal area (SI, appendix, figures S5(a)–(f)), together with similar patterns of diameter class distribution in terms of stem density, basal area and C-stocks shown by the exclosures further supports the important role of small-sized trees in carbon storage in the exclosures and young secondary forest (figures 5(a)–(c)). The relative contribution of small-size trees to AGB stocks depends on forest type and severity of the disturbance [71]. For instance, in secondary forest, trees <10 cm stem diameter (dbh) accounted for 19% [62] and 24% [72]. Another study also found that understory woody plants (dbh <4 cm) contributes 30% of total AGB in an old field succession and 17% in a young secondary forest [73]. Although trees <10 cm dbh can contribute considerably to AGB stocks in secondary and highly disturbed old growth forests, they are usually missing from the forest inventories (e.g. [8, 74]), lead to underestimate the forest biomass when forest inventory data are used, particularly in young secondary forest dominated by small-size trees [8, 59, 62].

The magnitude of estimated C-stocks in 3–7 years old exclosures exceeds the C-stock estimates in the CGL by about 50%, indicating the importance of exclosures to restore the degraded landscapes across the upper Blue Nile river catchment [16, 66, 75]. Estimated C-stocks in our study area were similar to estimated C-stocks in other grazing exclosures in northern Ethiopia [32, 66]. The estimated C-stocks were not linearly related to exclosure age, suggesting that landscape carbon pool recovery does not only depend on the duration of altered management, but it may also depend on other features of the biophysical and social systems within which they are implemented [67, 76]. Another study indicated that the legacy of the initial vegetation coverage at the site plays a considerable role in restoring the degraded landscapes and ecosystem process rates during tropical forest successions [76]. Among other species, Leucaena sp. is a dominant species in terms of carbon stock, especially in the KIK (3 yrs) and ENK (4 yrs) exclosure sites. Although Leucaena sp. is a multipurpose tree species, it is considered as an invasive species and is aggressively replacing indigenous trees in many parts of the world [77–79]. Hence, future management options should consider limiting the expansion of this species and, if possible, replace this species by indigenous tree species. Concerning carbon pool comparison between exclosures and CGL, future studies should consider increasing the number of observations from CGL, thereby evaluating the effectiveness of grazing exclosures in recovering degraded landscapes across the region.

5. Conclusions

This study presents the first mixed-species allometric equations for small-size trees in northern Ethiopia. The best model explained 82% of the variation in measured AGB. It produced the lowest bias and narrow ranges of errors across different diameter classes, compared to other generalized biomass estimation models from Ethiopia and elsewhere in Africa. This confirms that our model is robust and reliably estimates AGB and C-stock in grazing exclosures and young secondary forests dominated by small-size trees. Furthermore, the model has potential for application in other regions, where agro-ecological zones, tree-size distribution, species composition and site characters are similar to our study area. Exclosures accumulated large AGB and C-stocks than CGL, indicating the importance of grazing exclosures in assisting the processes of recovering the degraded landscapes and hence their suitability in mitigating climate change through sequestering atmospheric CO₂. Reported C-stock values can be used as a reference against which future estimates can be compared, thereby helping to investigate aboveground forest carbon dynamics in space and time under possibly different future climate conditions. Finally, future studies should also try to develop a mixed-species biomass estimation model for the remnant old growth and degraded secondary forests, thereby improving regional carbon assessment and accurate data availability.

Acknowledgments

We thank the Amhara Regional Agricultural Research Institute (ARARI) for their cooperation and facilitation of the research work. We are also grateful to the local communities in the study area and the Community Watershed Team (CWT) for their support during the field work. This study was conducted with the financial support of the Cuomo Foundation through the IPCC
scholarship. The contents of this document are solely the responsibility of the authors and do not represent the institutional position of the Cuomo Foundation and/or the IPCC.

ORCID iDs

Mulugeta Mokria  https://orcid.org/0000-0002-7812-8296

References

[1] Beer C et al 2010 Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate 329 834–8
[2] Kohl M, Lasco R, Cifuentes M, Jonsson O, K¨ohl M, Lasco R, Cifuentes M, Jonsson O, Korhonen K T, Mandhnenk P, De Jesus J and Sinistro G 2015 Changes in forest production, biomass and carbon: results from the 2015 UN FAO global forest resource assessment Forest Ecol. Manage. 2015 21–34
[3] Allen C D, Breshears D D and McDowell N G 2015 On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene Ecosphere 6 1–55
[4] Doughty C E et al 2015 Drought impact on forest carbon dynamics and fluxes in Amazonia Nature 519 78–84
[5] Gullison R E et al 2007 Tropical forests and climate policy Science 316 1136163–986
[6] Bongers F, Wassie A, Sterk F J, Bekele T and Teketay D 2008 Ecological restoration and church forests in northern Ethiopia J. Dryl. 1 35–44
[7] Teketay D, Lemenih M, Bekele T, Yemshaw Y, Feleke S, Tadesse W, Mages Y, Hunde T and Nigusu D 2010 Forest resources and challenges of sustainable management and conservation in Ethiopia Degraded Forests in Eastern Africa-Management and Restoration ed F Bongers and T Tennigkeit (London, New York: Earthscan) pp 19–64
[8] Mokria M, Gebrekirostos A, Aynekulu E and Brauning A 2015 Tree dieback affects climate change mitigation potential of a dry tropical forest in northern Ethiopia Forest Ecol. Manage. 344 73–83
[9] IPCC 2012 Managing the risks of extreme events and disasters to advance climate change adaptation A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change ed C B Field et al (Cambridge: Cambridge University Press) p 582
[10] Page Y Le, Morton D, Hartin C, Bond-Lamberty B, Pereira J M C, Hurtt G and Asrar G 2017 Synergy between land use and climate change increases future fire risk in Amazon forests Earth Syst. Dyn. Discuss. 8 1237–46
[11] Bonan G B 2008 Forests and climate change: forcings, feedbacks and the climate benefits of forests Science 320 1444–9
[12] IPCC 2007 Climate change 2007: The physical science basis Contribution of W orking Group I to the Fourth Assessment Report of the Intergovernmental Panel On Climate Change ed S Solomon, D Qin, M Manning, Z Chen, M Marquis, K B Avert, M Tignor and H L Miller (Cambridge: Cambridge University Press) p 996
[13] Corbera E, Estrada M and Brown K 2010 Reducing greenhouse gas emissions from deforestation and forest degradation in developing countries: revisiting the assumptions Clim. Change 100 355–88
[14] Corbera E and Schroeder H 2011 Governing and implementing REDD+ Environ. Sci. Policy 14 89–99
[15] AFR100 2016 First Regional Conference of the African Forest Landscape Restoration Initiative (AFR100) (www.afr100.org/sites/default/files/AFR100-Conference-Report.pdf)
[16] Seyoum Y, Birhane E, Hagaati N, Esmael N, Mengistu T and Kassa H 2015 Enhancing the role of forestry in building climate resilient green economy in Ethiopia: scaling up effective forest management practices in Tigray National Regional State with emphasis on area exclosures Addis Ababa (www.cifor.org/publications/pdf_files/Book) 2015
[17] Pan Y et al 2011 A large and persistent carbon sink in the world’s forests Science 333 988–93
[18] Hilmer U, Brauning A, Gebrekostos A and Huth A 2015 Impacts of precipitation variability on the dynamics of a dry tropical montane forest Ecol. Modell. 320 92–101
[19] Chave J et al 2014 Improved allometric models to estimate the aboveground biomass of tropical trees Glob. Change Biol. 20 3177–90
[20] Clark D B and Kellner J R 2012 Tropical forest biomass estimation and the fallacy of misplaced concreteness J. Veg. Sci. 23 1191–6
[21] Henry M et al 2013 GlobAllomeTree: international platform for tree allometric equations to support volume, biomass and carbon assessment iForest Biogeosci. Forest 6 236–30
[22] Vieilledent G, Vaudry R, Andriamanohisoa S F D, Rakotonarivo C B, Ebeling J and Rasamoelina M 2012 A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models Ecol. Appl. 22 572–83
[23] Rodrigues L, Junior N, Enged V L, Parrota J A and Galva A C 2014 Allometric equations for estimating tree biomass in restored mixed-species Atlantic Biota. Neotrop. 14 1–9
[24] Henry M, Picard N, Trotta C, Manly R J, Valentin R, Bernoux M and Saint-andr´e L 2011 Estimating tree biomass of sub-saharan African forests: a review of available allometric equations Silvae. Fern. 45 377–569
[25] Mekuria W, Langan S, Johnston R, Belay B, Amare D, Gashaw T, DEST G, Noble A and Wale A 2015 Restoring aboveground carbon and biodiversity: a case study from the Nile basin, Ethiopia Forest Sci. Technol. 11 86–96
[26] Tho 2004 Livestock sector brief (www.fao.org/ag/againfo/ resources/en/publications/sector_briefs/lsb_ETH.pdf. 2004) p 20
[27] Yalow S, Mul M, van Griesvnen A, Tefere E, Pries J, Schweitzer C and van der Zaag P 2016 Land-use change modelling in the upper blue Nile Basin Environments 3 21
[28] Mwendera E J J and Saleem M A M 1997 Hydrologic response to cattle grazing in the Ethiopian highlands Agric. Ecosyst. Environment. 64 33–41
[29] Mokria M, Gebrekostos A, Abiyu A, Van N oordwijka M and Brauning A 2015 Multi-century tree-ring precipitation record reveals increasing frequency of extreme dry events in the upper Blue Nile River catchment Glob. Change Biol. 23 2222–49
[30] Birhane E, Tredtly A C, Esthete A, Solomon N and Hailemariam M 2017 Can rangelands gain from bush encroachment? Carbon stocks of communal grazing lands invaded by Prosopis juliflora J. Arid. Environ. 141 60–7
[31] Chaturvedi R K and Raghubanshi A S 2012 Aboveground biomass estimation of small diameter woody species of tropical dry forest New Forest 44 509–19
[32] Mekuria W, Veldkamp E and Corre M D 2011 Restoration of degraded Forests in Eastern Africa-Management and Restoration ed F Bongers and T Tennigkeit (London, New York: Earthscan) pp 19–64
[33] Negash M, Starr M, Kanninen M and Berhe L 2013 Allometric equations for estimating aboveground biomass of Coffea arabica L grown in the Rift Valley escarpment of Ethiopia Agrofor. Syst. 87 955–66
[34] Kuyah S, Dietz J, Muthuri C, Jamnadass R, Mwangi P, Coe R and Neufeldt H 2012 Agriculture, ecosystems and environment allometric equations for estimating biomass in agricultural landscapes: i. aboveground biomass agriculture Ecosyst. Environ. 158 216–24
[35] IPCC 2006 2006 IPCC Guidelines for National Greenhouse Inventories, prepared by the National Greenhouse Gas Inventories Programme ed H S Egbelosten, L Baedna, K Miwa, T Ngara and K Tanabe (Japan: IGES) (http://www.ipcc-nggip.jges.or.jp)}
Aerts R et al 2012 Manual for Building Tree Volume and Biomass Allometric Equations From Field Measurement to Prediction (Rome: Food and Agricultural Organization of the United Nations, Rome, and Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Montpellier) p 215

Arlot S and Celisse A 2010 A survey of cross-validation procedures for model selection Stat. Surv. 4 40–79

Sampaio E, Gasson P, Baracat A, Cutler D, Parendo F and Costa K 2010 Tree biomass estimation in regenerating areas of tropical dry vegetation in northeast Brazil Forest Ecol. Manage. 259 1135–40

Sileshi G W 2014 A critical review of forest biomass estimation models, common mistakes and corrective measures Forest Ecol. Manage. 329 237–54

Ali A, Xu M, Zhao Y, Zhang Q, Zhou L, Yang X and Yan E 2015 Allometric biomass equations for shrub and small tree Silva. Fenn. 49 1–10

Ketterings Q M, Coe R, Van Noordwijk M, Ambagau Y and Ali A, Xu M, Zhao Y, Zhang Q, Zhou L, Yang X and Yan E 2015 Allometric biomass equations for shrub and small tree Silva. Fenn. 49 1–10

Ayers E, Denich M and Tsegaye D 2009 Regeneration forests: threats, opportunities and implications for their management Sci. Total. Environ. 551–552 404–14

Aynekulu E, Aerts R, Moonen P, Denich M, Gebrehiwot K, Zewdie M, Olsson M and Verwijst T 2009 Above-ground biomass estimation in regenerating areas of temperate forest trees and their implications for the management of forest landscapes Anal. Sci. Total. Environ. 84–97

Aynekulu E, Aerts R, Moonen P, Denich M, Gebrehiwot K, Zewdie M, Olsson M and Verwijst T 2009 Above-ground biomass estimation in regenerating areas of temperate forest trees and their implications for the management of forest landscapes Anal. Sci. Total. Environ. 84–97
[75] Park K H, Qu Z Q, Wan Q Q, Ding G D and Wu B 2013 Effects of enclosures on vegetation recovery and succession in Hulunbeier steppe, China Forest Sci. Technol. 9 25–32

[76] Lohbeck M, Poorter L, Martinez-Ramos M and Bongers F 2014 Biomass is the main driver of changes in ecosystem process rates during tropical forest succession Ecology 96 1242–52

[77] Hughes C. 1998 Leucaena leucocephala ssp. ixtahuacana The IUCN red list of threatened species (https://doi.org/10.2305/IUCN.UK.1998.RLTS.T37493A10053523.en)

[78] Orwa C, Mutua A, Kindt R, Jamnadass R and Anthony S 2009 Agroforestree database: a tree reference and selection guide Agroforestry 1–8 (www.worldagroforestry.org/sites/treedbs/treedatabases.asp)

[79] CABI 2017 Invasive Species Compendium (Wallingford: CAB International) (https://www.cabi.org/isc/)

[80] Ellison A M 2014 Experiments are revealing a foundation species: a case study of Eastern hemlock (Tsuga canadensis) Adv. Ecol. 2014 1–11

[81] Ellison A M et al 2005 Loss of foundation species: consequences for the structure and dynamics of forested ecosystems in a nutshell Front. Ecol. Env. 3 479–86

[82] Ellison A M, Barker-Plotkin A A, Foster D R and Orwig D A 2010 Experimentally testing the role of foundation species in forests: the Harvard forest hemlock removal experiment Methods Ecol. Evol. 1 168–79