Forest Ecology and Management 496 (2021) 119439

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Biomass of timber species in Central American secondary forests: Towards climate change mitigation through sustainable timber harvesting

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ARTICLE INFO

Keywords:
Secondary succession
Forest landscape restoration
Climate change mitigation
Forest management
National forest inventories
Nicaragua
Costa Rica

ABSTRACT

Sustainable management of secondary forests for timber production offers the opportunity to combine nature-based climate change mitigation with direct improvement of human livelihoods in the tropics, but this dual potential has rarely been explored. We characterized aboveground biomass (AGB) in secondary forests (SF) in Nicaragua and Costa Rica in whole stands (ecological potential), individual trees of timber species (total timber potential), and currently harvestable timber (harvestable timber potential). We also linked the three types of AGB potential to climate and soil factors. Data on 302 sample plots were collected, most from national forest inventories (NFIs) concerning 168 plots in Nicaragua and 134 plots in Costa Rica.

We analyzed data from individuals $\geq$20 cm dbh, estimating biomass from field measurements of stem diameters, and wood density and tree height estimates from the BIOMASS package in R. We obtained climate data from CHELSA, soil data from the ISRIC world soils database and determined the relationship between the three AGB potentials and environmental variables using exploratory principal components analysis and general linear mixed models (GLMMs).

A mean 51 Mg ha^{-1} AGB was found to be stored in trees $\geq$20 cm dbh in dry forests and 68 Mg ha^{-1} in wet forests. Maximum values were $>$ 250 Mg ha^{-1} in both biomes, similar to primary forest values from the NFIs. Timber potential was high at 84% of the mean ecological potential of the study plots, with 73% in the currently harvestable category. Overall, both ecological and total timber potential AGB were significantly higher in wet than in dry forests, whereas currently harvestable timber potential was significantly higher in dry than in wet forests. The best GLMMs showed $R^2 = 0.31$, 0.24 and 0.27 for ecological, total timber and harvestable timber potentials, respectively ($P < 0.0001$). All three models included soil clay and silt fractions, soil C/N ratio, mean annual precipitation and temperature seasonality. The GLMM for ecological potential included soil pH and climatic water deficit, while those for the two timber potentials included mean annual temperature. Overall, GLMMs indicate increasing timber AGB potential with increasing rainfall, decreasing climatic seasonality, and soil fertility. All three AGB potentials were significantly higher in Costa Rica than in Nicaragua in both biomes. This observed non-environmental “country effect” requires further study.

1. Introduction

Tropical forest area is decreasing at an alarming rate due to a combination of fragmentation, logging, and changes in land use in favor of agriculture and urbanization (Laurance et al., 2014; Lewis et al., 2015). It is estimated that deforestation caused the loss of 420 million hectares of forest between 1990 and 2020, more than 90% of which was in the tropics (FAO, 2020).

Destructive conventional logging is a major contributor to the decreasing forest area in the tropics. It is conducive to forest

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https://doi.org/10.1016/j.foreco.2021.119439
Received 7 January 2021; Received in revised form 4 June 2021; Accepted 5 June 2021
Available online 21 June 2021

degradation, which is an indirect driver of deforestation (Neves et al., 2019). Both deforestation and forest degradation contribute to greenhouse gas emissions. Even under sustainable management, after the first logging of old-growth forests (OGFs), felling cycles are not long enough to allow aboveground biomass (AGB) or timber stocks to return to their original values (Putz et al., 2012; Schwartz et al. 2017). Moreover, some studies have shown an increase in tree mortality after logging and silvicultural treatment (Finegan and Camacho, 1999; Dionisio et al., 2017). These factors contribute to decisions to convert forest to non-forest land uses (Laurance et al., 2014).

However, in some tropical regions, growing deforestation and degradation of OGF is paralleled by the increasing extent of secondary forest (SF) that regenerates naturally on large areas of private or communal fallow or abandoned farmland (Finegan, 1992; Chazdon, 2014; Chazdon et al. 2016). SF represents more than half the tropical forest area worldwide (Poorter et al., 2016). The increase in the SF area and the decrease in that of OGF has increased interest in SF in the literature and in policy making (Barlow et al., 2007; Chazdon, 2014). SFs are expected to significantly mitigate climate change due to their rapid accumulation of AGB and biodiversity loss due to their rapid recovery in species richness (Brown & Lugo, 1990; Poorter et al., 2016; Rozendaal et al., 2019). Although the control of OGF degradation and deforestation is of the highest priority, the value of the goods and services that can be provided by SF is increasingly recognized and even expected (Martin et al., 2013; Chazdon et al., 2016; Rozendaal et al., 2019). As is the case for OGFs (Putz et al., 2012), climate change mitigation and sustainable production objectives can and should be combined in the management of tropical SFs.

In this context, our study investigates the timber production and climate change mitigation potentials of SF in terms of three AGB metrics: total stand AGB (defined as the ecological potential), AGB of all timber species (defined as the total timber potential), and currently harvestable AGB of timber species (defined as the harvestable timber potential). In this article, 'timber species' refers to a set of tree species that are potentially harvestable and can be used as timber. Although SF delivers a suite of ecosystem services closely linked to forest biomass (Poorter et al. 2016), including timber production, it is nevertheless rarely tackled in the literature (Finegan, 1992 is an exception). The recovery time of forest characteristics during secondary succession may vary from a few decades for AGB and species richness to several centuries for species composition (Poorter et al. 2016; Chazdon et al. 2016; Meli et al., 2017; Rozendaal et al. 2019). SF may never recover the whole suite of OGF characteristics, or may take a different regeneration path depending on the degree of disturbance (Kammesheidt et al., 2002; Chazdon, 2014). Because of the slow recovery time of forest composition, the timber potential of SF is likely to differ significantly from that of the original OGF. SFs lack the large trees belonging to high-value timber species typical of OGF. Indeed, the characteristic SF timber species are mainly fast-growing species of lower wood quality than the slower growing species found in OGFs (Finegan, 1992; Adi et al., 2014). The international timber trade may also discourage timber production in SFs, as the timber species they contain are not competitive on the world timber markets (Bawa & Seidler, 1998; FAO, 2020), and on the rare occasions when timber production in tropical SF has been discussed, it has been connected to local markets in a community forestry context (Brown & Lugo, 1990; Finegan, 1992; Chazdon, 2014). International markets prefer OGF timber species because of their high quality and high value timber and prefer plantation species because they provide large volumes of timber of constant quality (Bawa & Seidler, 1998; FAO, 2020).

If SFs are perceived as lacking economic value, their long-term persistence is threatened by conversion to other more economically profitable land uses, often agricultural (Bawa & Seidler, 1998; Reid et al., 2017). In Central America, like in many tropical regions, guaranteeing the sustainability of SFs is thus a major challenge. For example, over the last six decades in southeastern Costa Rica, SFs have only had a short lifespan with 50% cleared in the first 20 years following land abandonment and 85% in the first 54 years (Reid et al., 2018). This has happened despite attempts to encourage their conservation with REDD + policies and payment for ecosystem services (Arroyo-Mora et al., 2014; Pagiola et al., 2007) and relatively recent regulations that create adequate legal frameworks for SF management.

Our interest in the timber potential of SF is based on the hypothesis that sustainable management for wood production may give added value to these vulnerable forest ecosystems, thereby contributing to the improvement of rural livelihoods, climate change mitigation and the achievement of long-term forest and landscape restoration goals (Ngo Bieng et al., 2021). At the same time, timber production in SFs may provide a complementary alternative for wood production, hopefully contributing to a decrease in the logging pressure on OGFs, and the resulting degradation and deforestation (Brown & Lugo, 1990; Bawa & Seidler, 1998; Fantini et al., 2019). Characterizing the combined climate change mitigation and timber potential of SF is therefore a crucial first step in maintaining and sustainably using SF cover in tropical areas. In landscapes under pressure, the persistence of SF offers a nature-based solution for forest landscape restoration and climate change mitigation.

We analyzed data from forest inventories and research projects in lowland SF in Costa Rica and Nicaragua. Central America was highly deforested due to the advance of the agricultural frontier in the period from the 1960s to the 1980s (Redo et al., 2012). Myers & Tucker (1987) estimated a forest loss of 20 million of ha between the 1950s and the 1980s at the level of Central America. Since the 1980s, forest cover has been partially restored in Costa Rica, mainly through secondary succession on abandoned pastures (Stan and Sanchez-Azofeifa, 2019). Deforestation continues in Nicaragua's Caribbean autonomous regions, but has been exacerbated by severe hurricane impacts in the last three decades (Redo et al. 2012; Aide et al., 2013; see globalforestwatch.org). Nicaragua's forest cover currently accounts for 26% of total land area, of which 43% is SF and 39% is OGF (Cuadra Cruz et al., 2015; Cuadra Cruz et al., 2018). Costa Rica's current forest cover is 52%, 36% of which is SF, while most of the country's OGF is in protected highland areas (Stan and Sanchez-Azofeifa, 2019). SFs of different degrees of maturity are therefore an important component of forest cover on private and communal land in both countries. SF is often managed by the landowners (Arroyo-Mora et al., 2014) whose objective may have been production (agricultural or forestry) or conservation (Cuadra Cruz et al., 2018). On private land, the potential use of SFs may improve their persistence in the Central American landscape. For example, in dry forest areas, cattle ranchers graze their cattle in SFs in the dry season (González-Rivas et al., 2006; González-Rivas et al., 2009; Godinot et al. 2020). SFs are therefore useful as a source of feed, but also of shade, which favors their conservation in agricultural landscapes.

Biomass recovery through natural secondary succession and its potential ability to contribute to climate change mitigation was quantified and modeled at the neotropical scale by Chazdon et al. (2016) and Poorter et al. (2016). Landscape-scale sequestration and storage of carbon through patch-scale sustainable management of SFs, i.e. a dedicated silvicultural management technique applied to patches of SF in landscapes that favors SF dynamics, is one alternative solution for long-term conservation of this mitigation potential. But what is the proportion of total SF AGB comprised by timber species? What proportion will therefore be lost through harvesting and must be recovered through appropriate silviculture and management of the stand and landscape? Which environmental factors influence variations in total and timber species AGB across landscapes?

In this paper, we provide some preliminary answers to these key questions. Our aim was to characterize timber species AGB as a proportion of the total AGB of SFs in Nicaragua and Costa Rica. We assessed the AGB of all species in 302 sample plots (ecological potential) and the AGB of timber species (timber potential). SF AGB is influenced by previous site use, plot age, and environmental factors (Brown & Lugo, 1990; Becknell et al., 2012; Chazdon, 2014; Poorter et al., 2016; Santiago-García et al., 2019). AGB recovery during secondary succession is typically faster in wet than in dry forests, probably due to increased water availability as measured by mean annual rainfall and climatic water deficit (Poorter et al. 2016). Measures of soil fertility such as cation exchange capacity CEC may also be positively correlated with AGB recovery rates (Toledo et al., 2011; Becknell & Powers, 2014). We consequently also assessed the relationship between environmental factors and the ecological and timber potential. We discuss our results in light of the differences between the two biomes, and the effects of the environmental variables. We also discuss management options consistent with increasing climate change mitigation and timber production potential during secondary succession, plus the desired impact on their sustainability and relevance for forest landscape restoration.

2. Methods

2.1. Study area

Here, we define secondary forest (SFs) as the woody vegetation that develops on agricultural land after it is abandoned or left fallow (Finegan & Nasi, 2004). CHELSA data (https://chelsa-climate.org/) report mean annual temperatures (MAT) ranging from 15 °C to 27 °C for Costa Rica and 18 °C to 30 °C for Nicaragua. Annual precipitation ranges from 1,475 mm to 5,070 mm in Costa Rica and from 900 mm to 4,200 mm in Nicaragua. Costa Rica has a very high relief (0 to 3,820 m above sea level) with a succession of Cordilleras (Guanacaste, Central and Talamanca), as does Nicaragua (0 to 2,438 m a.s.l.) with a central mountain range, and both have high volcanic activity (CIA, 2016). Both countries display dry and wet forests. We define dry forests as forests with 250–2,200 mm mean annual precipitation (Becknell et al., 2012). We define wet forests as forests with mean annual precipitation > 2,200 mm. Respectively 23.3% of forests are thus defined as dry in Costa Rica (Programa REDD/CCAD-GIZ – SINAC (2015a) and 18% in Nicaragua (MAGFOR & INAFOR (2009). The Nicaraguan landscape is characterized by the predominance of pasture, whereas the Caribbean coastal part is predominated by rain forests and wetlands, and the north-western part by a combination of pasture and savannah (MAGFOR & INAFOR, 2009). Outside protected areas, the Costa Rican landscape is characterized by a combination of fragmented secondary and primary forest patches located in crop and pastureland (Stan and Sanchez-Azofeifa, 2019).

2.2. Field sampling

Our study was based on a large set of national and local forest inventories covering the two countries. The dataset includes data from recent national forest inventories (MAGFOR and INAFOR (2009) for Nicaragua, and Programa REDD/CCAD-GIZ – SINAC (2015b) for Costa Rica) as well as experimental and private plots, giving a total of 302 plots. The plots ranged in size from 0.1 to 1.6 ha. Species identification in both inventory and research plots was carried out or coordinated by experienced botanists, mostly to species level, and at least to genus or family level. Verification of botanical identification made in the field was carried out at family level using the Missouri Botanical Gardens platform (https://www.missouribotanicalgarden.org/) and at the species level using the Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/). Tree diameters were measured at a height of 1.3 m above the ground. In 45% of the study plots, all trees ≥ 10 cm dbh (diameter at breast height, 1.3 m) were measured. In 55% of the plots, only trees ≥ 20 cm in dbh were measured. In the following analysis, to account for all the study plots, we considered only trees with dbh ≥ 20 cm. Tree height (H) was also measured in the field in 84% of the study plots.

2.3. Explanatory variables

One of the objectives of this study was to determine the effects of climate and soil on the ecological and timber potential. Climate variables at a spatial resolution of 1 km were obtained from CHELSA (https://chelsa-climate.org/) with the exception of climatic water deficit (CWD), which was obtained from http://chave.ups-tlse.fr/pantropical_allometry.htm. CWD is the difference between precipitation and evapotranspiration during the dry season. CWD is by definition negative and CWD = 0 means no water stress (Chave et al., 2014). Soil variables at a spatial resolution of 250 m were obtained from ISRIC world Soil Information (http://maps.isric.org/). All these variables are listed in Table 1.

In the data set we analyzed, following the definition of Becknell et al., (2012), the range of mean annual precipitation (250–2200 mm) that defines dry forests corresponds to strongly seasonal rainfall with a mean precipitation seasonality of 64% and a mean CWD of −450 mm yr^{-1}.

2.4. Definitions of ecological, total timber and harvestable timber potentials

In this study, we define ecological potential as the AGB of all the individuals inventoried in the plots. We define total timber potential as the AGB of all individuals belonging to timber tree species in the study plots. Finally, we define “harvestable timber potential” as the AGB of individual timber trees with dbh ≥ the current legal cutting diameter: 30 cm in Costa Rica (SINAC, 2017b) and 40 cm in Nicaragua (Comité Técnico Forestal, 2013). Timber species were identified using local and regional databases on forest products in Latin America (Malavassi, 2003; MAGFOR & INAFOR, 2009; SINAC, 2017a ; Piponiot et al., 2019). We used a final list of 935 tree species that are potentially harvestable and used for their timber. Some of these species, like *Cordia Alliodora, Trichospermum* sp, *Xylopia frutescens, Heliocarpus appendiculatus* and *Schizolobium parahyba* are well known and already sold in local and regional markets (Henao et al., 2015).

We excluded remnant trees from our calculations as their biomass is not produced during secondary succession but before land abandonment (Chazdon, 2014; Santiago-García et al., 2019). As the forest inventory data do not record the ages of SFs, we identified remnant trees on the

Table 1
Definition and source of the explanatory variables used in our statistical analyses.

Type of variable	Name of variable	Definition / unit	Source
Soil (0–200 cm)	C	percentage of carbon (%)	World database
	CEC	cation exchange capacity (mol/kg)	World database
	Clay	percentage (%)	World database
	N	percentage of nitrogen (%)	World database
	pH		World database
	Silt	percentage (%)	World database
	C/N	the ratio of carbon to nitrogen	Computed
Climate	anPR	mean annual precipitation (mm/yr)	World database
	MAT	mean annual temperature (°C)	World database
	Prsea	precipitation seasonality (coefficient of variation)	World database
	Tsea	temperature seasonality (standard deviation)	World database
	CWD	climatic water deficit (mm/yr)	World database

basis of their species and diameter (Santiago-García et al., 2019). Based on precise knowledge of the functional characteristics of each species, we identified species associated with primary forests that are rare in local SFs (for example, slow growing species). We also recorded the diameter of the remnant tree species identified in the SF study plots, as remnant trees often had a much larger diameter than the mean diameter of a given SF plot. We defined a threshold dbh above which a tree would be considered as remnant in each biome (dry and wet). For species not associated with secondary succession, the threshold dbh was determined by calculating the 97.5th percentile, i.e., the threshold corresponding to a dbh below which 97.5% of trees are included.

2.5. Above-ground biomass (AGB)

We estimated the AGB of 84% of the study plots for which we had field-measured values of height H using the generalized allometric model (equation 4) of Chave et al (2014), which uses tree dbh, H and wood density (WD, at the species level). WD values were estimated using data from the global WD database (Chave et al., 2009). For the individuals identified at the genus or family level, we used mean values for these levels calculated from the same database. This allometric model is valid for all types of tropical vegetation without observation of the effect of regional or environmental factors (Chave et al., 2014).

For the remaining 16% of the study plots for which we had no measured values of H, we estimated AGB using Réjou-Méchain's allometric equation (2017). This equation combines equations 4 and 6 from Chave et al. (2014) using dbh and WD. WD was again taken from the global WD database (Chave et al., 2009) for species, genus, or family. Réjou-Méchain's equation (2017) uses a bioclimatic stress variable E on which the generic diameter-height relationship linearly depends in order to correct for the absence of height (Chave et al, 2014). The variable E includes variations in temperature, precipitation and drought intensity.

The use of the Réjou-Méchain's equation was decided after comparing the results of three different allometric equations fitted to each biome that do not account for the height H of the trees: (i) Chave's equations (2005), (ii) Réjou-Méchain's equation (2017) and (iii) Brown's equations (1989). Using 84% of the plots for which we had the measured values of height H, we estimated the AGB from these three equations without taking the measured height H into account. We then selected the equation whose AGB values obtained were closest to the values obtained with Chave's equation (2014) calculated using the measured height values. Among the three equations tested, Réjou-Méchain's equation was the one that overestimated the AGB the least.

In this study, we therefore calculated the AGB of each tree using equation 4 (Chave et al. 2014) for 84% of the plots and using Réjou-Méchain's equation (2017) for the remaining 16%. The values of each tree were summed per plot to obtain the AGB of the plot in Megagrams (Mg). We transformed the AGB of each plot into hectares (ha) to obtain a standardized AGB in Mg ha^{-1} for each plot.

2.6. Data analysis

2.6.1. Distribution of the different potential AGB over the entire study area

We calculated the AGB values that account for each ecological, total, and harvestable timber potential defined. We compared the mean AGB across the two countries, and then across the dry and wet forest biomes using Student's T test.

2.6.2. Relationship between environmental variables and potential AGB

We first performed a principal component analysis (PCA) using all the environmental variables listed in Table 1 to assess the soil and climatic variables linked to timber potential. We used ANOVA and post-hoc Tukey's tests to determine if there were any significant differences in the centroid of the clusters of plots highlighted in the biplot based on the first principal components using environmental and country variables.

As mentioned above, due to the significant variation in the size of the plots (from 0.1 to 1.6 ha), we estimated a standardized AGB in Mg ha^{-1} for each plot. However, we did account for possible effects of different plot sizes on AGB variations by specifying plot size as a covariable in the variance functions of the general linear mixed models (GLMMs) we built.

We also included country as a random effect in order to account for the possible impact of the different years the inventories were performed in the two countries, i.e. in 2007–2008 in Nicaragua and in 2013–2014 in Costa Rica. We used multiple linear regression analysis in the GLMM framework to determine the relationship of each potential with soil and climate variables (Table 1). As NFI data do not include the age of the forest, we were unable to use forest age in our analysis. The regression analysis was preceded by a backward elimination test to select the environmental variables to be included in the models. We then compared the resulting models based on the Akaike information criterion (AIC) and the coefficient of determination (R^2).

All the analyses were carried out in R 4.0.3 (R Development Core Team, 2020).

3. Results

The final database includes 22,331 trees of which 97.9% are identified to the species level and 98.01% are identified when genus and family levels are counted. Among the 923 species identified in the database, according to the databases we consulted, 308 are timber species (see Appendix 1). Remnant trees removed from the analysis had a dbh $\geq$ 56 cm in dry SF and $\geq$ 64 cm in wet SF. Of the 302 plots, 168 were located in Nicaragua and 134 in Costa Rica.

3.1. AGB potentials

Overall mean ecological potential AGB was 62 ± 56 Mg ha^{-1} (range 1.2 to 330 Mg ha^{-1}, Table 2). The mean total timber potential AGB was slightly lower, 51.4 ± 53.7 Mg ha^{-1} representing 84% of ecological AGB (range 0.1 to 309.8 Mg ha^{-1}). The mean harvestable timber potential AGB was on average 44.8 ± 56.5 Mg ha^{-1} representing 73% of ecological AGB (range 0.35 to 296.6 Mg ha^{-1}).

Descriptive statistics suggest AGB potential differed between dry and wet biomes (Table 2). Ecological and total timber potentials AGB appear higher in wet SFs than in dry SFs. The difference in AGB accumulation in the two biomes varied depending on the potential concerned: for ecological and total timber potentials, we found respectively in average around 25.3% (17 Mg ha^{-1}) and 11.4% (6 Mg ha^{-1}) more AGB in wet than in dry SF, whereas for harvestable timber potential, we found around 3.6% (2 Mg ha^{-1}) AGB more AGB in dry than in wet SF. The difference between dry and wet forests decreased with the potential and was smallest for harvestable timber potential. Conversely, the AGB contributed by harvestable timber tree species was significantly higher in dry biomes than in wet biomes. This result is due a higher abundance of harvestable timber trees in dry SFs than in wet.

All three AGB potentials were significantly higher in Costa Rica than in Nicaragua in the two biomes (AGB distribution in the two countries is shown in Appendix 2).

3.2. Relationship between environmental variables and AGB potentials

The first two components of the PCA analysis of the three potentials explained 58.2% of the variance of the environmental variable data. PC1 explained 40.4% of total variance while PC2 explained 17.8% (Fig. 1; variable loadings on the two PCA axes are shown in Appendix 3).

PC1 represented an environmental spectrum along which the wet biome (negative scores) is clearly separated from the dry biome (positive scores). The wet biome was defined by high annual precipitation, low temperature and precipitation seasonality, and low CWD. Acid clay soils

Table 2
Descriptive statistics of above-ground biomass in plots containing dry and wet SF for each AGB potential (ecological, total timber and harvestable timber).

	dry					**wet**				
AGB potential	**mean**	**median**	**Q3**	**min**	**max**	**mean**	**median**	**Q3**	**min**	**max**
Ecological	51.04	36.31	72.9	1.21	259.47	68.32	52.53	93.24	2.53	329.93
Total timber	47.9	29.94	68.25	0.08	259.47	54.04	34.58	74.8	1.46	309.74
Harvestable timber	45.75	19.15	72.47	0.7	259.47	44.10	22.81	47.76	0.35	296.64

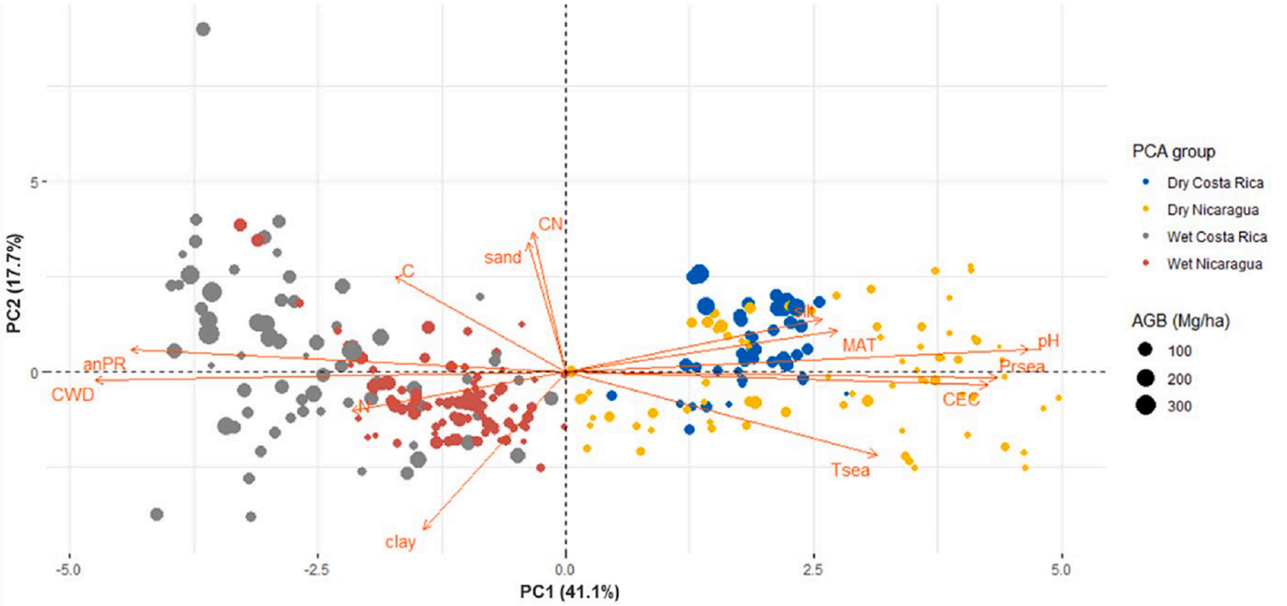

Fig. 1. Biplot of PCA analysis with environmental and country variables, representing the ecological potential (point size represents the total AGB per plot). As the biplots of global and harvestable timber potentials are similar, they are not shown here.

Table 3
Results of group comparison found on the principal component CP1 of PCA with the P-value (P) and the F statistic (F) of ANOVA. Different letters indicate significant difference between means of the different groups based on Tukey's post hoc test ($p < 0.05$).

ANOVA	**Ecological**	**Total Timber**	**Harvestable timber**	–	——	–
P	< 0.001	< 0.001	< 0.001			
F	734.27	735.96	678.09			
Tukey's test						
PCA groups	mean		mean		mean	
Dry Costa Rica	1.88	a	1.88	a	2.04	a
Wet Costa Rica	−2.62	b	−2.62	b	−2.56	b
Dry Nicaragua	2.64	c	2.63	c	2.48	a
Wet Nicaragua	−1.15	d	−1.18	d	−1.09	c

with low CEC, poor in silt but rich in C and N were mainly associated with the wet biome. The dry biome was defined by more marked seasonal climatic variation, silty, less acid soils with higher CEC (Fig. 1). PC2 represented a narrower environmental spectrum than PC1, and was mainly defined by the soil C/N ratio and variation in C and in the soil texture depending on the relative amounts of sand and clay.

The biplot in Fig. 1 suggests four distinct groups of plots, Costa Rican dry forest, Costa Rican wet forest, Nicaraguan dry forest and Nicaraguan wet forest. Two groups have negative scores on PC1, the wet SF plots in Costa Rica and the wet SF plots in Nicaragua. Dry forest plots have positive scores, and the Costa Rican plots are the most clustered. The different PCA axis scores of dry and wet forests suggest a climate effect on AGB, while the clustering of plots from each country suggest a country effect (see below). The AGB of the potentials thus did not appear to only be associated with climate but also with soil properties, mainly pH and CEC. It should be mentioned that in our dataset, the dry forest biome is represented by 40.9% of the plots in Nicaragua and 47.5% of the plots in Costa Rica.

ANOVA and Tukey's tests revealed a significant difference between the four groups identified in the PCA ($p < 0.001$, Table 3). PC1 enabled differentiation in pairs of four groups for ecological and total timber potential. However, no significant difference was found in harvestable timber potential between dry forests in Costa Rica and Nicaragua (see Table 3).

Separate linear regressions for the three AGB potentials produced the following results. As the soil texture variables sand, clay, and silt are very strongly collinear (variance inflation factor > 10,000), we removed sand from our analyses.

R^2 values were 0.31, 0.24 and 0.27 for the ecological, total timber and harvestable timber potentials, respectively ($P < 0.0001$; Table 4). Soil C, clay, silt (all three with negative effects) and the C/N ratio, (with a positive effect), were included in all three models, as were annual

Table 4
Multiple regression models predicting the three AGB potentials using the environmental soil and climate variables listed in Table 1.

AGB potential	Model	R^2
Ecological	$521.36 - 8.15C - 3.71clay - 23.78pH - 5.23silt + 2.48CN + 0.01anPR - 0.10tsea - 0.04CWD$	0.31
Total timber	$294.21 - 11.23C - 3.41clay - 5.03silt + 2.66CN + 0.01anPR + 3.22MAT - 0.10tsea$	0.24
Harvestable timber	$292.84 - 18.63C - 3.68clay - 4.28silt + 3.59CN + 0.01anPR + 2.85MAT - 0.12tsea$	0.27

precipitation (positive effect) and temperature seasonality (negative effect). Annual precipitation, CWD (positive effect) and soil pH (negative effect) were included in the best model for ecological potential although their individual effects were not significant. Overall, the regressions provide statistical confidence in the relationships between the AGB potentials and environment described on the first axis of the PCA: AGB tends to be highest in the wet biome with its high annual precipitation, low climatic seasonality, and acid clay soils, and decreases across the environmental spectrum to the dry biome with its seasonal climate and less acid soils. The models for timber AGB potentials included in addition to the previous set, MAT with a positive effect, although it was not significant in the best model for harvestable timber potential. Accounting for the plot size as a covariable in the variance functions and accounting for the random country effect did not improve the fit of the model and were therefore not included in the selected models.

4. Discussion

For this study we collected a large set of field data on secondary forest (SF) vegetation in Nicaragua and Costa Rica mainly from national forest inventories, and environmental data from online platforms. For individuals with a dbh $\geq$ 20 cm, we estimated total aboveground biomass (AGB) of SFs which represented their ecological potential for AGB accumulation. We also determined the proportion of total AGB belonging to timber species, both total and currently harvestable. These proportions represent the potential for accumulating AGB with direct value for sustainable forest management as well as to achieve climate change mitigation objectives. Overall, ecological and total timber potentials were higher in wet SFs on infertile soils than in dry forests (respectively $\sim$ 17 and 6 Mg ha^{-1}), while harvestable timber potentials were high in the two biomes (>40 Mg ha^{-1}), and differed only by 2 Mg ha^{-1} between both. The variation in all three potentials was explained by multiple regression models including climate and soil variables that together characterize the major environmental gradient between dry SFs, which have relatively low AGB, and wet SFs, where AGB is higher.

4.1. Estimating AGB using national forest inventory data

Plots included in the two national forest inventories (NFIs) represented 84% of our total of 302 plots. Sampling in the NFIs was systematic and sample size was adjusted to achieve acceptable degrees of error per forest type for estimation of national-scale data (MAGFOR & INAFOR, 2009; Programa REDD/CCAD-GIZ – SINAC, 2015). The NFIs therefore provide high-quality data for studies like ours, but have two disadvantages. First, neither country recorded either forest age or previous land use – key sources of uncertainty when estimating and modeling SF AGB (Chazdon et al., 2016) - and second, the minimum dbh of 20 cm used by Nicaragua means it is impossible to directly compare our results with those of the many studies that use dbh > 10 cm.

4.2. The secondary forests studied here have a significant timber potential that deserves to be known and valued

We established that total and harvestable timber potentials account for respectively 84% and 73% of the ecological potential. This result highlights the significant potential for timber production of SFs in both Costa Rica and Nicaragua. Given that SFs represent a high percentage of the forest cover outside protected areas in both countries, our results show that their AGBs have significant current and future timber potential. To our knowledge, our study is the first to evaluate the proportion of recovered biomass and the sequestered carbon it contains as a basis for sustainable timber production and AGB storage, contributing to the conservation of the SFs. High-profile studies with a subcontinental scope have highlighted the potential for biomass recovery and carbon sequestration in neotropical SFs (Chazdon et al. 2016, Poorter et al. 2016). These studies have focused on what in the present study, we call ecological potential. The ecological potential of SFs – AGB recovery and climate change mitigation – is therefore widely recognized, whereas their potential for timber production is not. The high timber potentials suggest a role for SFs in sustainable management for timber production, which would also contribute to climate change mitigation.

We found many species (308 species) with timber potential in our study area, among which some are already exploited in Central America, such as *Cordia alliodora* which is particularly abundant in our plots, *Trichospermum mexicanum*, *Xylopia frutescens*, *Heliocarpus appendiculatus* and *Schizolobium parahyba* (Henao et al., 2015; see Appendix 1). However, the vast majority of these species have no valued timber potential currently. The real timber potential of tropical SFs we highlighted in this study needs be known, improved and valued. Examples of local recognition of SF timber potential have been documented (e.g. Smith et al., 2001; Henao et al., 2015), but considerable improvements, for example related to management strategies, and economic and political framework, are still required.

Specifically accounting for management strategies, silvicultural treatments that enhance timber tree dynamics are needed to promote SF timber potential. In our study, we found 308 timber species that represented approximately 34% of the ecological diversity of the study plots. Adequate management focusing on increasing timber species will be consistent with biodiversity conservation (Kammesheidt et al., 2002). Possible silvicultural treatments include the protection of tree seedlings of species identified as being of commercial value (González-Rivas et al., 2009; Neves et al., 2019); enrichment planting using seedling of the identified species to stimulate dynamics and increase the timber potential (Neves et al., 2019; Griscom, 2020). Beside enhancing and securing timber potential in vulnerable SFs, these management strategies will also contribute to climate change mitigation and forest landscape restoration.

Depending on the economic and political frameworks applied, improvements could include the creation of enabling environments, for example incentives that support the survival of SF such as payments for ecosystem services for ecological potential or grants for the implementation of silvicultural treatments (Pagiola et al., 2007; Reid et al., 2018). Costa Rica modified its forest law in this way to allow effective silviculture and harvesting of SFs on private land: a pioneering initiative in the tropics (SCIJ, 2016). In Nicaragua, specific regulations for the management of SFs remain to be established.

According to timber markets, technical adjustments will require modification of international market requirements so that the timber potential of SF is recognized, by extending the list of acceptable commercial species to include SF species. In that case, it will also be necessary to reduce the minimum standard commercial diameter in sawmills (Bawa and Seidler 1998). The development of timber certification specific to SFs will certainly help enhance and secure timber potential in SFs.

4.3. AGB variation across dry and wet biomes

In this study, the AGB potentials we defined differed between dry and wet SF and were adequately modeled in terms of both climatic and soils variables. Our results are based on the sampling efforts of NFIs and regional projects with an equivalent number of plots in the two countries (56% in Costa Rica), biomes (42.7% in dry biomes), and biomes in the two countries (40.9% in Nicaragua dry forest, 47.5% in Costa Rica dry forest). The highest ecological and total timber potential was found in wet SF despite their infertile soils. In contrast, the harvestable timber potential was significantly higher in dry than in wet SFs. This reverse trend may be linked to a difference (although minimal) in the abundance of timber trees between the two biomes. As the NFI data do not include forest age we were unable to use this key variable in our models. However, modeling by Chazdon et al. (2016), suggests that SFs in the age range 1–60 years predominate in Costa Rica and Nicaragua.

Our results support the observed relationship between the AGB of SF and climate (Poorter et al. 2016). Wet tropical climates promote the accumulation of AGB thanks to high water availability (high annual precipitation and low CWD) (Poorter et al., 2016) and low seasonal temperature variations resulting in an almost constant growing season for trees (Toledo et al., 2011; Becknell et al., 2012). Also, increasing climate seasonality drives increasing community mean wood density, WD, in neotropical SFs, which, if it means lower growth rates, may be a proximate cause of lower biomass accumulation (Poorter et al. 2016; 2019). Community mean WD represents the average value of all the trees present in a community. After land abandonment in wet forests, species with high WD values increase in abundance over time, while the reverse occurs in dry forests. A high WD may reflect drought tolerance in the dry biome where the start of succession is hindered by environmental factors. These differences in the evolution of the community mean WD between biomes lead to the convergence of community WDs over time as the vegetation cover accumulates (Poorter et al., 2019).

Although previous work in both SF and OGF has shown climatic variables to be strongly correlated with AGB (Toledo et al., 2011; Becknell et al., 2012; Poorter et al., 2016), this was not the case in our study, despite the strong variations of climatic variables across our plots (Appendix 4). Indeed, the marginal effects associated with annual precipitation and seasonal temperatures are very low (0.01 and 0.10–0.12). This result suggests that soils differences between dry and wet forests contribute to AGB accumulation in Central American SFs.

4.4. Relative importance of soil properties as predictors of AGB variation

We found a clear positive relationship between AGB and water availability and our PCA confirmed the expected relationship between high rainfall and acid, infertile soils. The PCA also showed variation in soils within wet and dry biomes and overall, our regression models suggest that soil variables complement climate in making an important contribution to AGB variation.

The effect of soil fertility variables (texture and nutrients) on AGB at different geographic scales in tropical SF and OGF is the subject of debate. Variables like CEC and K have been shown to be positively correlated with AGB in SF (Becknell & Powers, 2014; Poorter et al., 2016; Santiago-García et al., 2019) and in OGF (Laurance et al., 1999; Baker et al., 2009; Gourlet-Fleury et al., 2011) whereas other studies found little or no effect of soil fertility on AGB (Clark & Clark, 2000; DeWalt & Chave, 2004; Toledo et al., 2011).

In our study, correlations between AGB variation and soil fertility were negative. Indeed, modeling of the relationship between AGB and environmental factors revealed a significantly positive direct correlation between each potential AGB and soils poor in clay, silt, and C with a high C / N ratio. Infertile soils are associated with the wetter climates in our data and in a regional study, where Poorter et al. (2016) found that AGB recovery in SFs increased with water availability. The negative correlation with soil fertility in our study could be related to the efficiency of forests in wetter climates in using soil nutrients. Indeed, when the climatic conditions are favorable/advantageous as is the case in wet SFs, trees are more efficient in the use of nutrients from poor soils (Herrera & Finegan, 1997).

The negative correlation between AGB variation and soil fertility could also be related to the impact of non-environmental variables, leading to more AGB accumulation in less fertile soils. Indeed, differences in AGB found in the two countries may respond to a non-environmental “country effect”, a possible set of historical and socio-economical variables that require further study (Redo et al., 2012; Aide et al., 2013).

It is important to note that in our study, the explanatory soil variables obtained from ISRIC may overestimate or underestimate values due to the lack of geographic precision. What is more, ISRIC does not provide variables that are considered to be limiting for AGB production and storage, such as phosphorus and potassium (Quesada et al., 2012).

5. Conclusions

Assessing the proportion of secondary forest (SF) above-ground biomass (AGB) provided by timber species is a valuable way to analyze the potential for sustainable management of SFs with combined mitigation and production objectives.

For such analyses, modern NFIs provide large unbiased field data sets with botanical identification. NFI data combined with traditional research plot data and environmental data available online, are invaluable in advancing our understanding and in enabling efficient management of the potential of SFs. Future NFIs should consider obtaining forest age and previous land use data for SFs, either through contact with forest owners or by modeling.

SFs in Central America may have significant potential for sustainable management with combined objectives. As sustainable timber production depends on market conditions, it will be necessary to combine evaluation of the ecological and timber potentials of the vegetation with the development of value chains for the timber species typically found in SFs.

As the ecological and total timber potentials of Costa Rican and Nicaraguan SFs are higher in wet than in dry biomes, active restoration which would enhance secondary succession in dry SFs, should have priority when designing forest landscape restoration in degraded dry biomes. Non-environmental historical and socioeconomic factors, which we define here as a “country effect”, may have an important impact on SF AGB and require further study.

Declaration of Competing Interest

The author declare that there is no conflict of interest.

Acknowledgements

This study was funded by the CGIAR Research Program on Forests, Trees and Agroforestry (FTA). We would like to thank all the financial partners who supported this research through their contributions to the CGIAR Fund. To view a list of donors to the Fund, visit: http://www.cgiar.org/about- us / our-funders / http://www.cgiar.org/about-%20us/our-funders/

We thank SINAC (*Sistema Nacional de Área de Conservación*); OEFo network (*Observatorio de Ecosistemas Forestales de Costa Rica),* mainly the Costa Rica Technological Institute (TEC) and national university (UNA); CATIE’s BS project led by Jean Pierre Morales and his representatives Leonel Coto and Juan Serrano Molina; and CATIE’s Posgrado School which provided some useful data.

We also thank the national forest inventory of Nicaragua, and Iris Saldívar Gómez of the Nicaragua national herbarium of the University of Central America (UCA) in Nicaragua and Vicente Herra for reviewing the species identification in the Costa Rican and Nicaraguan inventories.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119439.

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