

## Biomass accumulation and carbon sequestration in a reforestation project in La Gamba, Costa Rica

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Tropical reforestation is increasingly seen as important to provide ecosystem services, including climate regulation, carbon dioxide sequestration, and biodiversity conservation. To optimize the management of active reforestation projects, it is important to be clear about the goals and to compare the effect of reforestation on ecosystem services as well as the efficiency of the project in terms of costs, land area or other limiting resources. These effects will depend on many factors, including species selection. In the Finca Amable reforestation project in La Gamba, Costa Rica, different combinations of trees were planted in replicated plots. We monitored the growth of trees during the first six years and present here the results on biomass accumulation and carbon sequestration. We tested the effect of using different allometric models to predict biomass, and use a global model that includes tree diameter and height. After approximately five years, above-ground biomass of the planted trees had reached 13.5–59.6 t ha<sup>-1</sup> (mean 36.4), which corresponds to a CO<sub>2</sub> sequestration of 64 t ha<sup>-1</sup>. This is high compared to natural regeneration, but the comparison is limited by the few comparable data on very young secondary forests in the region and the effect of site factors. Considerable uncertainties also remain in the best allometric models, which could be improved by more detailed measurements of tree allometries.

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Die Wiederbewaldung in den Tropen wird zunehmend als wichtiger Beitrag zu Ökosystemdienstleistungen wie Klimaregulation, CO<sub>2</sub>-Sequestrierung und Erhaltung der Biodiversität anerkannt. Um eine Wiederbewaldung optimal durchzuführen sollten zunächst deren Ziele klar definiert und müssen im Verlauf sowohl der Effekt auf Ökosystemdienstleistungen als auch die Effizienz in Bezug auf Kosten, Landnutzung und anderen Ressourcen quantifiziert werden. Diese Effekte hängen von verschiedenen Faktoren einschließlich der Auswahl der Baumarten ab. Im Wiederbewaldungsprojekt Finca Amable bei La Gamba in Costa Rica wurden verschiedene Kombinationen von Bäumen in replizierten Versuchsflächen gepflanzt, das Wachstum in den ersten sechs Jahren gemessen und daraus Biomasseakkumulation und CO<sub>2</sub>-Sequestrierung berechnet. Nach einem Vergleich verschiedener allometrischer Modelle zur Berechnung der Biomasse wurden ein generelles Modell, das Baumdurchmesser und -höhe einschließt, als das geeignetste ausgewählt. Etwa fünf Jahren nach dem Auspflanzen der Bäume hatte die oberirdische Biomasse in den einzelnen Flächen 13,5–59,6 (Mittel: 36,4) t ha<sup>-1</sup> erreicht, was einer CO<sub>2</sub> Sequestrierung von durchschnittlich 64 t ha<sup>-1</sup> entspricht. Dies ist hoch im Vergleich zu einer natürlichen Regeneration ohne aktivem Setzen von Bäumen, allerdings ist der Vergleich limitiert weil es wenige vergleichbaren Daten von jungen Sekundärwäldern in der Region gibt. Auch beim besten allometrischen Modell bleiben beträchtliche Unsicherheiten, die durch detailliertere Messungen von Bäumen reduziert werden könnten.

**Keywords:** Costa Rica, reforestation, functional diversity, biomass growth, allometric biomass model.

## Introduction

Tropical forests store about 37 % of the global terrestrial carbon pool (DIXON et al. 1994), account for approx. 33 % of net primary production (BONAN 2008) and 60 % of gross photosynthesis (BEER et al. 2010), and tropical rainforests are the most biodiverse biome on earth (BARLOW et al. 2018). In addition, they provide many vital ecosystem services including climate regulation and resources that sustain the livelihoods of millions of people (MILLENIUM\_ECOSYSTEM\_ASSESSMENT 2005). Increasing human impact on tropical forests via hunting, degradation, conversion to other land uses, fragmentation and impacts of climate change threaten this diversity as well as ecosystem functions and services (LEWIS et al. 2015). Tropical forest degradation is a major source of carbon emissions contributing to the increasing atmospheric CO<sub>2</sub> concentration and thereby global warming. Emissions from tropical forest loss and degradation were estimated at approx. 2.9 Pg (or billion tons) of carbon per year at the beginning of this century (MITCHARD 2018). Currently, the effect of tropical forest areas on atmospheric CO<sub>2</sub> thus appears to be approximately neutral. Without the sinks, the increase of atmospheric CO<sub>2</sub> would be faster still, but if forest degradation were reduced or forest recovery were increased, tropical forests could become important net carbon sinks.

The need to restore deforested and degraded land for reasons that include biodiversity conservation, climate mitigation, water protection and security of livelihoods has gained increasing support. International initiatives such as REDD+ (Reducing Emissions from Deforestation and Forest Degradation, ALEXANDER et al. 2011) and the Convention on Biological Diversity ([www.cbd.int](http://www.cbd.int)) focus global efforts to restore degraded tropical land. For instance by the end of 2018, 57 countries and private organizations have pledged to bring 170 million hectares of degraded and deforested land into restoration with the goal of reaching 350 million hectares by 2030 ([www.bonnchallenge.org](http://www.bonnchallenge.org)). Costa Rica alone has committed to restore 1 million hectares by 2020. Landowners in Costa Rica are encouraged to contribute to this goal through a program of payments for ecosystem services (including carbon sequestration, biodiversity and water protection) managed by the Fondo Nacional de Financiamiento Forestal (Fonafifo, [www.fonafifo.go.cr](http://www.fonafifo.go.cr)).

When disturbance stops or agricultural land is abandoned, the forests will eventually regrow. These secondary forests that are re-growing on previously deforested land were neglected for a long time as ecosystems that do not match primary forests in terms of biodiversity and complexity. They consequently received limited scientific interest, but are recognized today as important refuges for many species where primary forests have been lost or are strongly reduced and fragmented, and regrowing forests are the most important terrestrial carbon sink (CHAZDON 2014). In 2008 second-growth tropical forest covered 2.4 million km<sup>2</sup> in Latin America. These lands could sequester 31 Pg CO<sub>2</sub> over 40 years through natural succession or assisted regeneration, and permitting forest regeneration on 40 % of often low-productivity pastures could capture an additional 7 Pg CO<sub>2</sub> (CHAZDON et al. 2016).

Left alone, tropical forests will eventually regrow under most circumstances, but how fast they recover their biomass, diversity, and other ecosystem functions and services depends on many factors. Soil degradation, the loss of the soil seedbank, absence of seed sources, the harsh microclimate or very competitive herbaceous vegetation may hinder regrowth and arrest succession (WALKER 1994; SLOCUM et al. 2004; ELGAR et al. 2014). A study

in the Australian wet tropics found that compared to natural regeneration of rainforests, actively reforested sites increased substantially faster in wood volume (and thus biomass) and woody plant diversity, the latter largely independent of the dispersal mode (SHOO *et al.* 2016). By contrast, the diversity of non-arboreal plants (vines, epiphytes and ferns) increased only slowly with stand age in the actively reforested as well as the naturally regrowing sites. In situations where natural regrowth is slow or when there is a strong interest to restore the ecosystem services and biodiversity of the forest rapidly, actively planting trees may be the strategy of choice.

Since actively planting a forest is more costly than natural forest recovery, the advantages need to be weighed against the costs. Avoiding failure requires detailed information on obtaining seeds or seedlings, raising seedlings in nurseries, and planting and caring for the trees during the first years. For a number of tropical trees of commercial value, this information is readily available, but for many others our knowledge on how to manage them is scant or absent (but see ROMÁN *et al.* 2012 and BARQUERO PALMA *et al.* 2012 for Central American trees). Many reforestation projects have contributed important insights into the practical management of tree species and human-assisted forest recovery (LAMB 2011; VAN BREUGEL *et al.* 2011a). For most regions, however, only a fraction of the local forest species has been tested and the trees planted are mostly from relatively few species that are easily available and known to grow well, which results in a forest with a strongly selective species-composition that is often not representative of a natural old-growth forest. Apart from the successful management of a reforestation, decisions about the aim of the project also need to be taken when selecting trees. The purpose of reforestation could, for instance, be carbon sequestration, protection of biodiversity, creating a biological corridor, scientific studies, commercial timber and non-timber products for local or non-local markets, or non-commercial forest products and services (LAMB 2011). While many forests will provide all of these functions to some degree, there is no forest that maximizes all. For instance, a young forest composed of a few fast-growing species will initially sequester more carbon but will be less diverse than a forest that includes many fast- and slow-growing species.

Overall, higher tree diversity tends to result in higher productivity through complementarity in resource use (MORIN *et al.* 2011). This has recently been confirmed from a subtropical reforestation project, where tree diversity per plot ranged between 1 and 16 species (HUANG *et al.* 2018). However, a global study of mature tropical forests found that the relationship between diversity and productivity depends on the spatial scale, and at a scale of 1 ha negative relationships were more common (CHISHOLM *et al.* 2013). Whether diversity is positively or negatively related to growth depends on the selection of individual species in a comparison (which may have intrinsically higher or lower growth) and on the complementarity of species. When the species number is high but their requirements are very similar, they will likely compete with each other similarly to individuals of a single species. If, on the other hand, the species are functionally very diverse, the complementarity and thus the positive effect of diversity is likely greater.

To test the effect of functional diversity independent of species diversity, trees were planted in plots with the same number of species per plot but with different numbers of functional groups in a reforestation project on Finca Amable close to La Gamba, Costa Rica. We do not evaluate growth performance of individual tree species here, but ask if functional types of trees differed in their growth and if a combination of different functional types had an

effect on plot-based tree biomass accumulation without changing the number of species. In addition, the analysis of the first five years of growth on Finca Amable presented here serves to estimate the carbon sequestration potential of this and other reforestation projects in the region, and provides a basis to compare growth and carbon sequestration with natural succession or other land management strategies.

## Material and Methods

The reforestation site Finca Amable (Fig. 1) is located in the vicinity of the village La Gamba, close to the La Gamba field station in the Puntarenas province, SW Costa Rica (8°42'03.78"N 83°12'06.14"W). It is part of the local reforestation project COBIGA (Corredor Biológico La Gamba), whose main purpose is to establish a network of reforested areas connecting the protected lowland rainforest of the Golfo Dulce region with the lower montane rainforests in the Fila Cal mountain range. Finca Amable was previously a cattle pasture dominated by the introduced pasture grass *Paspalum fasciculatum*. The site is flat at approximately 70 m above sea level. Average annual temperature is 28.3°C and annual rainfall is 5930 mm (WEISSENHOFER et al. 2008). December to April is less rainy, but there is no month with < 100 mm of rainfall (which is often used to characterize a dry season) and most months receive > 200 mm. The natural vegetation is a humid lowland



Fig. 1: Aerial photograph of Finca Amable, the reforestation sites is outlined in red. Photo: A. WEISSENHOFER, March 2018. – Abb. 1: Luftbild der Finca Amable, die Wiederbewaldungsfläche ist rot umrandet. Foto: A. WEISSENHOFER, März 2018.

rainforest. Soils are plastic loamy clays and can be flooded during the rainy season. Because of the stagnant water resulting in partly anoxic soil, drainage of the area was improved by digging several parallel ditches with a distance of approx. 50 m and some smaller ditches perpendicular to these to drain towards a river.

Trees were planted on approx. 13.7 ha in a rectangular pattern with a spacing of  $3.5 \times 4$  m in plots of  $6 \times 6$  trees separated by at least one tree row between plots. Seeds or seedlings had been collected in local forests and were grown in a nursery for several weeks. Planting was done mostly during the wetter season with trees 30–100 cm tall. For planting and the first 2–3 years afterwards, grass and other competing vegetation including vines and lianas were manually cut around each tree several times per year. Trees were first planted between 2012 and early 2014, but trees that had died were replaced until 2015.

We classified species into three functional groups. Legumes (Caesalpiaceae, Fabaceae and Mimosaceae, “LEG”), non-legume trees with high wood density ( $> 0.5 \text{ g / cm}^3$ , “HWD”), and non-legumes with low wood density ( $< 0.5 \text{ g / cm}^3$ , “LWD”). Wood density data were obtained from the wood density database (ZANNE et al. 2009) with some own local measurements for species not included in the database. In each plot of  $6 \times 6$  trees, nine species with four individuals each were planted. While the number of species was therefore constant, we modified the number of functional groups by planting nine spe-



Fig. 2: Finca Amable in La Gamba before tree planting (2012, note the drainage ditch) and in 2015, 2016 and 2018. Note the low-branching trees in 2016 and 2018 (*Inga* sp.), which made diameter measurement at breast height impractical. – Abb. 2: Die Finca Amable in La Gamba vor der Pflanzung 2012 (mit Drainagegraben), 2015, 2016 und 2018. Bei den tief verzweigenden Bäume 2016 und 2018 (*Inga* sp.) wurde die Messung der Durchmesser nicht in Brusthöhe durchgeführt.

cies of only LEG, HWD or LWD, any combination of two functional groups with four or five species per group, or all three functional groups with three species per group. These seven combinations of functional groups were planted in a total of 56 plots. Originally, each combination should have been planted with eight replicates but due to tree mortality and species not available at the time of planting, the number of replicates is variable. Trees that had died in the first two years were replanted with the same species as far as possible, or another species from the same group if the same species was not available or had a high mortality rate and was therefore considered unsuitable for the local conditions. Trees that died later or where the replacement also died were not replaced again.

Trees in plots were measured at or soon after planting and again in 2013, 2015, 2016, 2017 and 2018 (Fig. 2). Due to time constraints, ten of the younger plots could not be re-measured in 2017, as goes for nine plots in 2018. Tree diameter was generally measured at breast height (1.3 m above soil surface), except when trees were branching below that height or when they were very irregular at 1.3 m, in which case the diameter was mostly measured below the lower branches and where the stem was terete. Tree height was measured with a marked pole to a height of approximately 4 m and with a laser rangefinder (Vertex IV, Haglöf, Sweden or TruPulse 350R, Laser Technology, Centennial CO) for taller trees.

### Biomass allometric models

Biomass was estimated using published allometric models. CHAVE *et al.* (CHAVE *et al.* 2014) present global models based on 4004 tropical trees from old-growth or secondary forests whose biomass was measured (usually by measuring the volume or fresh weight and drying subsamples of the tree) and related to height, diameter at breast height and wood specific gravity of individual trees. Their best pantropical model is:

$$\text{Equ. 1: } \text{AGB}_{\text{dh}} = 0.0673 \times (\rho D^2 H)^{0.976}$$

with  $\rho$ : wood specific gravity, D: diameter at breast height (dbh, in cm) and H: tree height (in m).

When tree height is not available, which is challenging to measure in closed tall forests, an alternative model uses dbh and a factor scaling for height, which depends on the climate:

$$\text{Equ. 2: } \text{AGB}_d = \exp(-1.803 - 0.976 * E + 0.976 * \log(\rho) + 2.673 * \log(D) - 0.0299 * (\log(D))^2)$$

For the climate in La Gamba,  $E = -0.0959$ .

This global dataset from 58 sites spans from trees > 5 cm dbh to large forest trees but is certainly biased towards smaller size classes. This likely makes biomass estimates for large trees less reliable, but the trees we studied were comfortably within the range covered by the dataset.

Allometric models for 26 species in a Panamanian reforestation project were presented by VAN BREUGEL *et al.* 2011b. Given that the trees were also growing in an open reforestation site (in contrast to trees from the CHAVE *et al.* dataset) and included some of our species or genera, the allometric model derived from the Panama data may be more appropriate for the trees in La Gamba. The sampled trees of these 26 species had a maximum dbh between 3.8 and 26.5 cm, whereas the largest tree in the plots sampled in La Gamba measured 53 cm dbh and 78 trees (3% of stems but 23% of basal area) had reached a dbh > 26 cm in

2018 (Fig. 3). Species-specific models differ substantially among species (Fig. 4). However, hardly any of their species-specific models can be used for our species, and we therefore used the overall model from VAN BREUGEL *et al.* 2011b.

$$\text{Equ. 3: } \text{AGB}_{\text{vb}} = \exp(-1.13 + 2.267 \cdot \log(\text{dbh}) + 1.186 \cdot \log(\text{WSG}))$$

and compared it to models Equ. 1 and 2. The VAN BREUGEL model does not include tree height and all models include wood density, which scales nearly linearly with biomass.

To compare the effect of using different models, we calculated biomass for each tree using the CHAVE models with and without height (Equ. 1 and 2) and the VAN BREUGEL model (Equ. 3).

For trees with buttresses or a broader lower stem, diameter for growth or biomass models is generally measured above the buttresses. The young trees we measured never had buttresses above 1.3 m, but branching at lower heights or irregular stems at 1.3 m was common, which forced a diameter measurement below 1.3 m (Fig. 2). This was frequently the case in *Inga* spp., *Zygia longifolia*, *Croton schiedeanus*, and *Vitex cooperi*. Given that the diameter will be somewhat greater than if measured at 1.3 m in a regular stem, this might result in an over-estimate of the biomass. Since *Inga* spp. were planted very often in the reforestation and have high biomass, we explored the potential implication of non-standard diameter measurements on biomass estimates. Stem taper, the gradual decrease of stem diameter with height above ground, has been measured in many trees and follows a rather uniform pattern (BURKHART & TOMÉ 2012), but for measurements below 1.3 m, where stems can broaden substantially more than described by standard taper functions, this is not feasible without specific measurements.

AGB of the trees within individual plots was scaled to 1 ha by dividing by 36 (6 × 6 trees) and multiplying by the number of trees per ha using the spacing between trees (10,000 m<sup>2</sup> / (3.5 m × 4 m) = 714). Biomass was converted to CO<sub>2</sub> absorbed using a carbon content in biomass of 0.48, typical for tropical wood (MARTIN & THOMAS 2011), and the carbon to

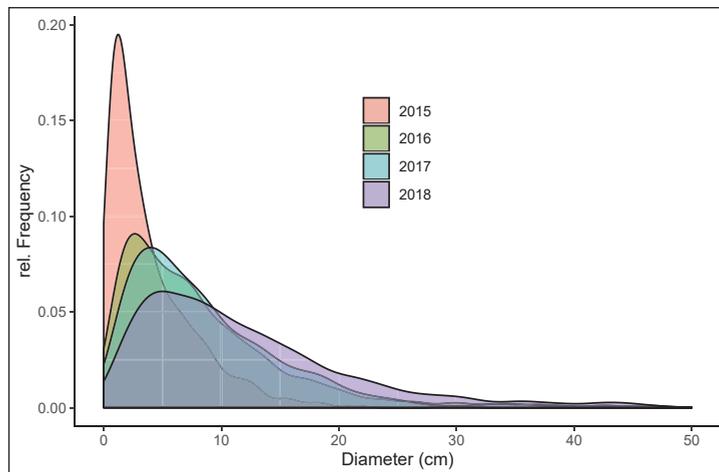


Fig. 3: Breast height diameter distributions in years 2015–2018 of trees on Finca Amable planted between 2012 and 2015. – Abb. 3: Verteilung der Brusthöhendurchmesser der auf der Finca Amable gepflanzten Bäume in den Jahren 2015–2018.

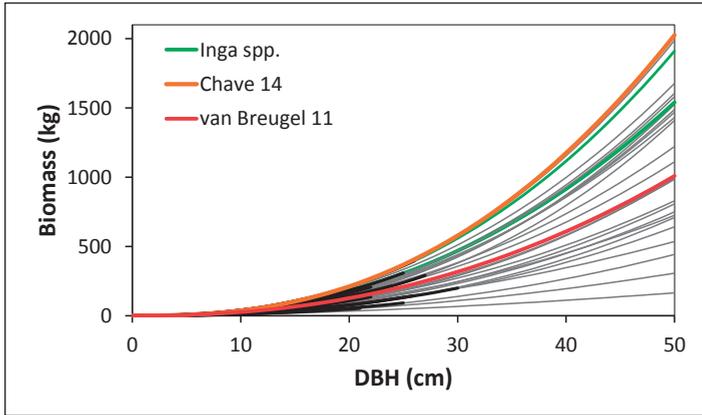


Fig. 4: General allometric models of CHAVE et al. (2014, Equ. 2) and the mixed-species models by VAN BREUGEL et al. (2011b). The other lines are allometric regressions for individual species (green for two *Inga* spp.) by VAN BREUGEL. Black lines show the diameter range of the data covered by VAN BREUGEL and thin grey lines extend the regressions beyond the data. – Abb. 4: Allgemeines allometrisches Modell nach CHAVE et al. (2014, Equ. 2) und das Modell von VAN BREUGEL et al. (2011b). Die anderen Linien entsprechen allometrischen Regressionen einzelner Arten (grün für zwei *Inga* spp.) nach VAN BREUGEL. Schwarze Linien entsprechen den Regression im Datenbereich, der von VAN BREUGEL abgedeckt wird, graue Linien gehen über diesen Datensatz hinaus.

CO<sub>2</sub> conversion factor of 3.66. One ton of biomass thus equates to 1.76 t CO<sub>2</sub> absorbed. Change in root biomass and soil carbon is difficult to measure and was ignored here. The age of the plot was the average time since the individual trees comprising each plot were planted.

To test if plot type (i.e. the composition of various functional groups) had an effect on AGB growth, we calculated a mixed effect model (LME) with AGB as the predicted variable, plot type and age as fixed factors, and age nested within plot-ID as random factor. Age and AGB were scaled by dividing by the root mean square because variables strongly differing in magnitude can bias LMEs. The LME was calculated using the R-function lmer and has the form:  $AGB \sim \text{plot-type} * \text{age.s} + (1 + \text{age} | \text{plot-ID})$ .

## Results

We first tested the differences between the global biomass model (CHAVE et al. 2014) with or without using tree height, and the local model for a young reforestation site (VAN BREUGEL et al. 2011b). Given that *Inga* spp. had become large trees that contribute substantially to biomass and have distinctly non-linear diameter: height relationships, we also visualized if the biomass estimates in *Inga* are more affected by including height or not. Over most of the size-range of the trees measured, the global biomass model without height yielded higher biomass estimates than the model including height (grey dots are above the 1:1 line in Fig. 5, note that the axes are on log-scales, so a relatively small deviation from the 1:1 line translates into substantial differences in biomass estimates as shown in the insert of Fig. 5). *Inga* spp. did not differ from the other trees in this respect. The global model based on dbh accounts for the variation in the height:

diameter relationship by using a factor related to the local climate. The comparison with the model including height suggests that this factor is not perfectly suited for our dataset, i.e. would overestimate tree height. This is plausible because trees in the young reforestation site likely invested less in height growth than trees in closed forests, which were mostly used for the global biomass model. The VAN BREUGEL model gave higher biomass estimates for small trees than the global model with height, while for larger trees the estimates were quite similar (along the 1:1 line). The VAN BREUGEL allometries are based on smaller trees (mostly < 20 cm dbh, Fig. 4), and extrapolating biomass estimates beyond the data range of the model is problematic. Although only a small proportion of trees we measured were > 20 cm dbh, these do account for a substantial proportion of biomass. For these reasons we use the global model with height to assess biomass accumulation per plot.

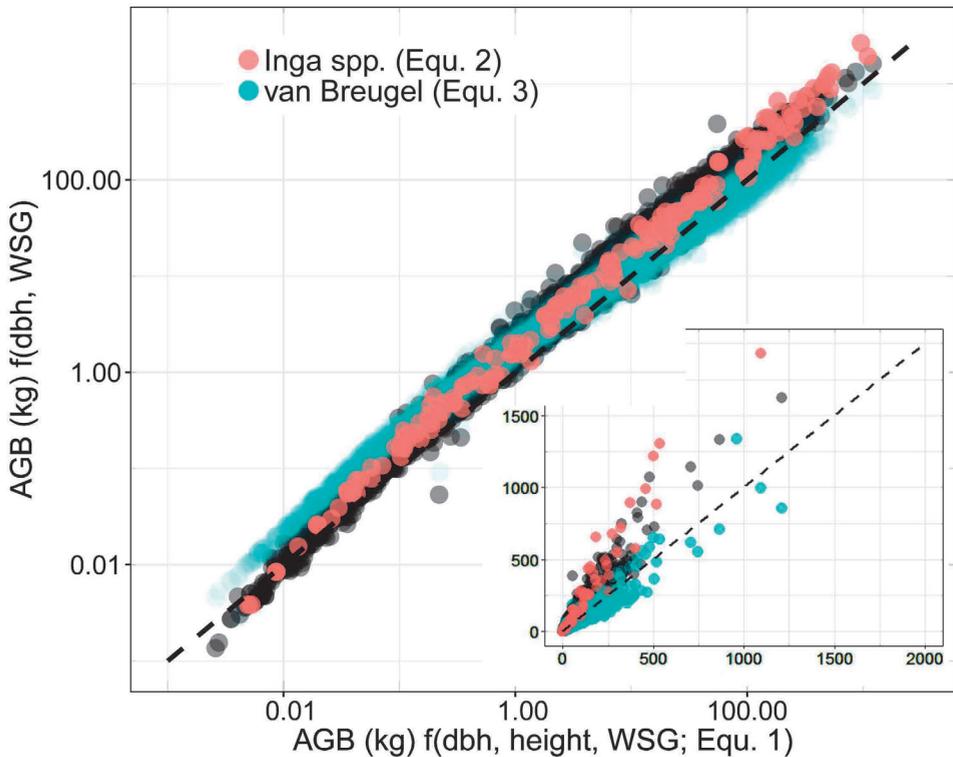


Fig. 5: Comparison between above-ground biomass (AGB) estimates based on diameter, wood specific gravity (WSG) and height (Equ. 1) against estimates based on diameter and WSG only (Equ. 2; grey symbols). Blue symbols compare the Equ. 1 with the VAN BREUGEL model for all trees (Equ. 3) and red symbols represent Equ. 2 for *Inga* spp. only. The insert shows the same data on a linear scale to highlight potential absolute errors. – Abb. 5: Oberirdischen Biomasse (AGB) berechnet aus Durchmesser, spezifischer Holzdicke (WSG) und Baumhöhe (Equ. 1) im Vergleich zur Berechnung, die nur auf Durchmesser und WSG basiert (Equ. 2, graue Symbole). Blaue Symbole vergleichen Equ. 1 mit dem VAN BREUGEL Modell für alle Bäume (Equ. 3), rote Symbole entsprechen Equ. 2 für *Inga* spp. Das Insert zeigt die gleichen Daten auf einer linearen Skala, um die absolute Größe der Fehler darzustellen.

Trees of some species tend to branch at low height (Fig. 2) so they were measured below 1.3 m, where the diameter is larger. To correct for this bias, we first compared the diameter: height correlation of trees measured at 1.3 m with the correlation of trees measured below 1.3 m. As expected, the diameter < 1.3 m was higher for a tree of the same height than the dbh (Fig. 6). We therefore corrected the diameter for trees not measured at 1.3 m by assuming that the diameter linearly decreased from ground level (0 m) to breast height (1.3 m) by 40 %. This is the best estimate so that the relationship between height and the estimated diameter is similar to the one between height and diameter measured at breast height (Fig. 6), which is the basis for all biomass calculations. This is not a perfect solution, but appears to be a viable way around the difficulty of measuring diameter in these trees, at least with the data available.

In April 2018, the average time since planting of the trees of each plot was between 3 and 5.5 years (Fig. 7). Biomass accumulation was low in the first two years, but afterwards increased substantially. Plots that were between 4.5 and 5.5 years old had reached an AGB of 12.5–52.2 t / ha (mean 35.7). The variation in biomass accumulation within any plot type (composition of functional types) was substantial and appeared to be greater than the variation between plot types. Indeed, in the mixed effect model, plot type (i.e., the func-

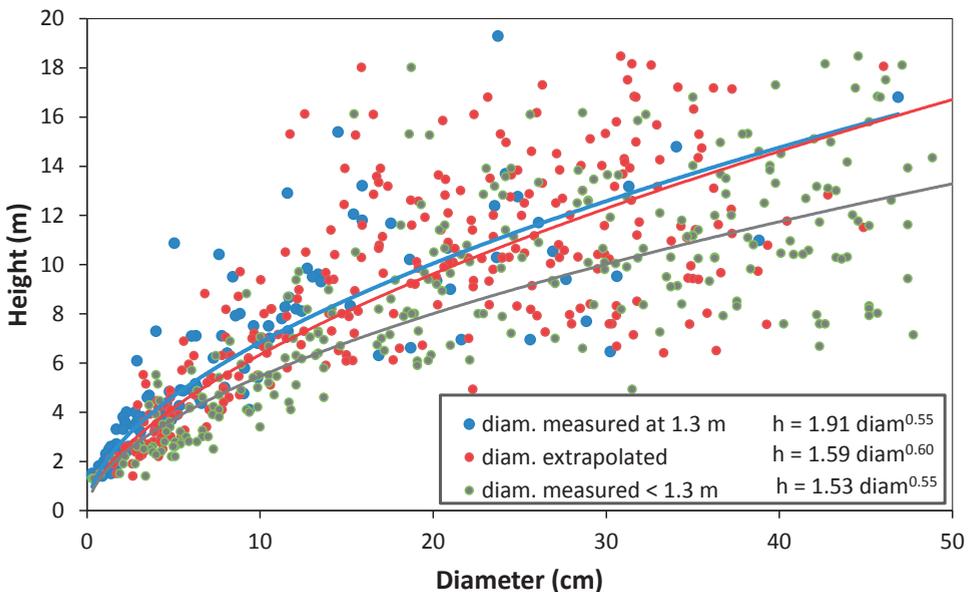


Fig. 6: Diameter: height relationships of *Inga* trees at the Finca Amable reforestation trial, measured 2016–2018, to illustrate the dbh-estimate for trees where the diameter was not measured at 1.3 m. Blue symbols and regression line show the diameter : height correlation for trees that were measured at 1.3 m; green symbols are diameter : height for trees measured below 1.3 m and red symbols are the same trees with corrected diameters (see text for details). – Abb. 6: Durchmesser: Höhen-Verhältnis für *Inga* auf der Finca Amable, gemessen 2016–2018, zur Illustration der Abschätzung des Brusthöhendurchmessers für die Bäume, deren Durchmesser nicht in 1.3 m gemessen wurde. Blaue Symbole und Regressionslinie: Bäume, die in 1.3 m gemessen wurden, grüne Symbole: Durchmesser : Höhen-Verhältnis für Bäume, die unter 1.3 m gemessen wurden, und rote Symbole entsprechen den selben Bäumen mit korrigiertem Durchmesser (Details im Text).

tional composition of trees) did not affect biomass accumulation ( $p > 0.4$ ). Surprisingly, plots with low wood density (LWD) species and with LWD plus legumes were increasing biomass particularly slowly, but only two plots of each variant had been planted successfully, these were rather young because they were planted somewhat later and their biomass also lay within the large biomass variation of the other plot types (Fig. 7). In plots where *Inga* was planted, these trees accounted for a large part of total AGB (compare to small symbols in Fig 7 for biomass without *Inga*), although the biomass of some plots without legumes was similar.

Remarkably, biomass in a few of the plots with high biomass in 2017 decreased somewhat or had not increased in 2018. Inspection of the original data showed that a few very large trees, mainly *Inga*, had decreased in estimated height and biomass. Although their diameter continued to increase, the height was substantially reduced in 2018 because, as noted in the field, large parts of the crown had broken off. This would not have been seen by us-

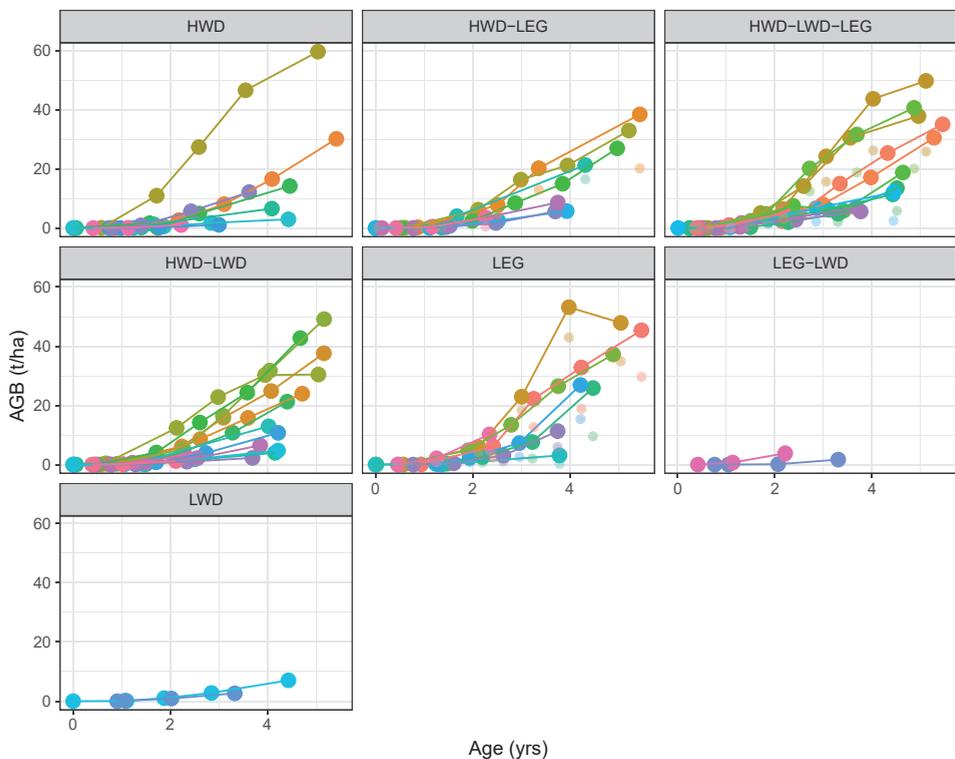


Fig. 7: Biomass accumulation over the first five years after planting in plots with different combinations of three functional groups (HWD: high wood density, LWD: low wood density, LEG: legumes). Individual plots within the panels are distinguished by symbol color and connecting lines. Small opaque symbols represent biomass excluding *Inga* spp. – Abb. 7: Biomasseakkumulation während ersten fünf Jahre nach der Pflanzung auf Versuchsflächen mit unterschiedlichen Kombinationen von drei funktionellen Gruppen von Bäumen (HWD: hohe Holzdicke, LWD: niedrige Holzdicke, LEG: Leguminosen). Die einzelnen Versuchsflächen innerhalb einer Teilgrafik sind durch unterschiedliche Farben und durchgezogene Linien gekennzeichnet. Kleine, semi-transparente Symbole entsprechen der Biomasse ohne *Inga* spp.

ing the diameter measurements alone. Similarly, a number of larger trees had broken off or been uprooted and had re-sprouted by 2018. In these cases, diameter and / or height were not useful to estimate their (remaining) biomass and these individuals were omitted from biomass estimates (i.e. treated as completely dead trees). Future surveys will show if and how damaged trees recover.

## Discussion

A biomass of 35.7 t ha<sup>-1</sup> corresponds to a sequestration of 61.8 t CO<sub>2</sub> ha<sup>-1</sup>. In 2018, all planted and surviving trees in approximately 2/3 of the total area were measured (3834 trees), which includes trees in the plots as well as trees between plots. Their combined biomass was estimated at 194.8 t, which corresponds to a CO<sub>2</sub> sequestration of 342.2 t. This does not include trees < 1.3 m and all spontaneously regenerating vegetation. The small trees would contribute very little to biomass and in 2018 the spontaneous regeneration included very few larger trees, so the underestimate in the above-ground biomass would be very minor. Also not accounted for is below-ground biomass, which is likely to contribute more but is hard to measure and mostly not included in biomass or carbon sink estimates. If we apply the average root: shoot ratio of 0.2 recorded in four young tropical moist forest plantations (MOKANY *et al.* 2006), the biomass and C sequestration would increase by 20%. This is likely a conservative estimate and other compilations report higher root: shoot ratios for tropical trees (WARING & POWERS 2017). The few studies looking at below-ground biomass during secondary succession of tropical forests show that it increases similarly to above-ground biomass and may reach 50% of mature forests after 30–40 years (MARTIN *et al.* 2012). By contrast, soil carbon is affected by forest disturbance much less than AGB and hardly changes during succession (MARTIN *et al.* 2012).

### **How does the AGB accumulation of the active reforestation compare to natural succession and tree monocultures?**

A large compilation of AGB in tropical secondary forests found a rapid accumulation of biomass, particularly during the first 40 years, after which forests had recovered more than 50% of the biomass of old-growth forests (POORTER *et al.* 2016, using Equ. 2). This dataset includes a number of very young plots that can be compared to the age of trees and plots we measured. Average AGB of forests reported to be 5 yrs old was 46.6 t / ha, somewhat larger than Finca Amable plots of the same age. However, the POORTER *et al.* data includes sites where large remnant trees were likely present at age 0 (L. POORTER, pers. comm.) and thus show an unrealistically high biomass at a very young age. Two local secondary forest plots around La Gamba of 5–6 years and 12 years had estimated AGB of 16 and 41 t / ha, respectively, which is low compared to the reforested plots, though the age estimate may also not be very accurate (OBERLEITNER 2016, using Equ. 2). From the rather few comparable data of secondary forests of the same age as Finca Amable plots, it thus appears that growth is greater than or at least in the upper range of natural regeneration. If the plots are re-measured in a few years, it should become clearer if and how the biomass growth compares to secondary forests in the region and elsewhere.

Monocultures of fast-growing species might increase biomass faster than mixed-species plantations that focus on biodiversity. Trial plantations with monocultures of six tree spe-

cies close to Buenos Aires (province Puntarenas, Costa Rica) had produced AGB up to 147.3 t / ha (ARIAS et al. 2011) after six years. While monocultures of the two exotic species tested (*Gmelina arborea* with 147.3 t and *Pinus caribea* with 85.7 t) clearly grow faster than the multi-species reforestation plots we studied, biomass growth of the other (native) species (31.8–76 t after six years) was comparable to several species combinations in Finca Amable (up to 60 t after five years, Fig. 7). To achieve the goal of high carbon sequestration it is thus not necessary to use monocultures when a more diverse tree community can sequester as much. Of course, differences between tree growth in the reforestation at Finca Amable and other tree plantations or also natural regeneration sites will also be due to differences in soil, local climate, or management of the plantation and not only the selection of tree species. To analyze these factors requires comparing multiple sites, which should be done in the future but was beyond the scope of our work.

### Improving biomass estimates

Tree biomass estimates strongly depend on the allometric model (LETCHER & CHAZDON 2009; VAN BREUGEL et al. 2011b), thus the potential error in plot-level AGB propagated via the choice of the model is substantial. Establishing species-wise models for each region is not feasible and nearly all forest biomass estimates in diverse tropical forests therefore rely on general models. Using the same model for different stands to be compared at least reduces the bias when comparing plots, even if the absolute values may be biased. Short of cutting and weighing trees, the models we used may be improved somewhat by more detailed measurements of individual trees. Diameter is the minimum measure taken and wood density data are available for many species and are also rather easy to measure. In light of the large discrepancy between the CHAVE 2014 model with and without tree height (Fig. 5), it may be worthwhile to adjust the model to be more suitable for trees growing in open sites or to use models based on biomass measurements of such trees, particularly when height measurements are not available. Tree height is the next most common parameter to measure and will improve the accuracy of our estimates. More detailed measurements of tree allometries, including crown radius or stem taper, might improve models still more. Since the stem and crown shape of *Inga* differs from most other species planted and since these are large and common trees, such detailed but also time-consuming measurements should start with this genus. Airborne or terrestrial laser scanning might further improve the accuracy of data on forest structure and tree allometries substantially in a very time-efficient way and, if available, could greatly improve the accuracy of biomass estimates in the future (TAYLOR et al. 2015; PALACE et al. 2016).

Dead trees on Finca Amable are no longer replaced and more will eventually die. Concurrently, spontaneous regeneration adds species and biomass. In the young reforestation site, the contribution of spontaneous regeneration is rather insignificant, at least for biomass. With time, the contribution of these plants will increase and spontaneous regrowth should be monitored in addition to the planted trees to characterize the effect of reforestation management on ecosystem recovery.

This first evaluation of the development of the young forest has been looking at forest biomass only. Carbon sequestration is one, but not the main aim of the reforestation project COBIGA, whose focus is mainly the protection of biodiversity. By planting more than 100 different tree species, the tree diversity is certainly much higher than in secondary

forests of similar ages and comparable to that of old-growth forests. To understand the effect of high tree diversity on the diversity of non-arboreal vegetation and fauna, it would be worthwhile to monitor the change in these groups with time and in comparison with natural succession and old-growth forests.

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