Benjamin Wadham-Gagnon
Diana Sharpe

ESTIMATING CARBON STOCKS IN TROPICAL HARDWOOD PLANTATIONS

Using species-specific allometric regressions and non-destructive parameters to estimate above-ground biomass for six native tree species in Panama

Submitted to Dr. Ibáñez
April 27, 2006
ENVR 451

TABLE OF CONTENTS

INTRODUCTION

1.1 Tropical Plantations as Carbon Sinks:

Increasing levels of atmospheric carbon dioxide are a matter of growing concern, principally because of their probable link with global climate change. As a result, there is intense interest in measuring and modeling the global carbon cycle to try to predict and hopefully mitigate potential future changes in climate.

Tropical forests are an important carbon sink. Undisturbed Neotropical forests are estimated to hold 76.86×10^9 Mg of organic matter, a significant portion of which is carbon (Brown et al. et *al.* 1989). However, deforestation and other land use changes in the past several decades have resulted in significant carbon emissions from theses sinks (Brown et *al.* 1989). For example, it is estimated that 1.6±1.0 GT of carbon year are released every year due to tropical land use changes (Schimel et *al*. 1996, cited in Nelson et al. et *al.* 1999). Deforestation has been rampant in Panama in the past few decades, with national forest cover plummeting from 70% in 1950 to 38% in 1980 (West and Augelli 1989). At the same time, regeneration of forests – either through natural overgrowth of abandoned pasture, or through planned reforestation – has the potential to reduce these emissions. In the Amazon, for example, 47.6% of deforested land is now covered with secondary regrowth (Nelson et al. et *al.* 1999). As a result, recent research has focused on the potential of reforestation in increasing carbon sequestration, and thus slowing climate change associated with carbon dioxide emissions (Harmon 2001). Several reforestation projects have been introduced on abandoned agricultural lands in tropical countries (Kraenzel et *al.* 2003). In the next few years, carbon credits may be distributed to landowners actively managing plantations (Harmon 2001). The proper functioning of the carbon credit system will require a profound knowledge of the carbon cycle dynamics in hardwood plantations, and a reliable means of quantifying biomass and carbon sequestration.

1.2 Estimating Carbon Stocks in Tropical Plantations:

A major challenge in modeling carbon sequestration in tropical plantations is estimating total above ground biomass (AGB), which is where a significant portion of the

carbon in forest ecosystems is stored. A certain amount of carbon is also sequestered in the root systems of trees, however little is known regarding these subterranean carbon stores due to the paucity of inventories on below-ground biomass (Raich and Nadelhoffer 1989).

The most precise way to measure AGB for a stand is through destructive harvest methods, i.e. by felling and weighing a representative sample of trees. Unfortunately, this procedure is destructive and time consuming. Not only are the cut trees removed from the forest, but the felling and extraction process may seriously injure neighboring trees and undergrowth. Furthermore, trunks, branches and leaves contain different concentrations of carbon, nitrogen, and water. It is therefore important to determine how each tree's mass is distributed into these structural categories, which implies long, meticulous, and time-consuming work on the field.

Fortunately, it has been shown that strong correlations exist between AGB and both tree diameter and tree height (Overman et *al.* 1994, Brown et *al.* 1989). Therefore allometric models can be developed to predict AGB from easily measurable variables such as diameter, height, and wood density. Such models have the potential to protect plantations from unnecessary destruction and save time on the field, which should potentially reduce AGB analysis costs to plantation owners. Whenever possible it is desirable to use species-specific models because they increase the precision of AGB estimates by accounting for differences in tree architecture and wood density between species (Ketterings et *al*. 2001).

To the best of our knowledge, all previous work on allometric models for estimation of AGB in the tropics has focused on natural forests. Because of the high levels of biodiversity typically observed in natural tropical forests, and the difficulty identifying many tropical tree species, species-specific models are very impractical for estimates of biomass in natural forests. Not surprisingly therefore, most models developed thus far have not been species-specific (e.g. Chave et *al.* 2005, Ketterings et *al.* 2001, Overman et *al.* 1994, Brown et *al*. 1989). In contrast to natural forests however, in plantations, all species are known and are easily located because they have been planted according to a fixed pattern. Furthermore, most plantations contain far fewer species than natural forests. Thus for plantation studies, species-specific allometric

models impose no significant extra field work and do not entail any risks of error due to false species identification.

Over a dozen different equations exist in the literature for estimated AGB in natural tropical forests, and tens more have been developed for temperate tree species (Ter-Mikaelian et *al.* 1997). In a recent review, Chave and colleagues reported that diameter at breast height (DBH), height, and specific wood density (SD) are the most important predictors of biomass (Chave et *al*. 2005). Indeed, most published allometric regressions incorporate these three variables in some combination. Of the three parameters, DBH is the most easily measurable, consistently reported, and highly correlated with biomass. As a result, the most widely reported allometric equations are power relationships of the form: $DW = \alpha DBH^{\beta}$.

While height has been incorporated in many models (e.g. Nelson et *al.* 1999, Brown et *al.* 1989, Chave et *al.* 2005), some authors argue against its use in regression equations. Height is very difficult to measure in closed-canopy forests, and is consistently underestimated in the field (Nelson et *al.* 1999). Furthermore, some studies have shown that incorporating height does not add much accuracy to models (Ter-Mikaelian et *al.* 1997, Nelson et *al.* 1999). The difficulties of measuring height may be reduced in more widely-spaced plantations, especially young plantations, because tree crowns are easily visible.

The use of specific wood density (SD) in regression models has also been somewhat controversial. Chave and colleagues (2005) found that SD was an important variable in all regressions and improved multiple-species estimation models significantly. However, a separate study by Nelson and colleagues (1999) found that SD was not very useful for predicting biomass in single-species regressions (Nelson et *al.* 1999).

1.3 Biodiversity and ecosystem productivity

An important consideration in modeling global carbon fluxes, and quantifying the relative contribution of plantations is that carbon sequestration may be correlated with species richness. The importance of biodiversity in regulating ecosystem properties and processes, such as primary production, is hotly debated. While most ecologists agree that a minimal number of species is required to sustain an ecosystem (Loreau 2001), there is

much contention concerning the effects of increasing species richness on vital ecosystem processes such as carbon sequestration, primary production, nutrient retention, decomposition, and soil respiration. Several theories have been proposed to relate biodiversity to ecosystem functioning. The species redundancy hypothesis predicts that above a critical level of diversity, species are functionally redundant, and thus increases in diversity beyond this point will have little effect on ecosystem processes. (Lawton and Brown et al. 1993, cited in Wardle et al. 1997). The ecosystem rivet hypothesis contends that all species contribute to an ecosystem in some way; thus increasing diversity will influence ecosystem function (Ehrlich and Ehrlich 1981, cited in Wardle et al. 1997). The idiosyncratic hypothesis also proposes that biodiversity affects ecosystem function, but in an unpredictable way, due to the complexity of the underlying mechanisms (Lawton 1994, cited in Wardle et al. 1997). Finally, the insurance hypothesis claims that biodiversity serves as a form of "insurance" or buffer against environmental fluctuations, and thus enhances community stability. (Loreau 2001).

Numerous experimental studies have been undertaken to test the above-mentioned hypotheses, most of them in temperate grassland ecosystems. Most have found a positive relationship between primary production and species richness. For example, a large-scale experiment at 8 different European grassland sites found a positive log-linear relationship between above-ground plant biomass and species number (Hector et al. 1999). However; other studies have generated contradictory findings. For example, litter-mix experiments conducted by Wardle and colleagues showed that increasing species diversity of plant litter from 2 to 8 species did not have a clear positive effect on either decomposition rate, or nitrogen dynamics (Wardle et al. 1997).

The relationship between diversity and ecosystem functioning is further obscured by the fact that functional group diversity, rather than species number per se, may regulate ecosystem processes (Loreau, 2001). Studies in Mediterranean grasslands and northern forests suggest that ecosystem properties depend on the functional characteristics of dominant plants species rather than biodiversity (Grime 1997).

Two main mechanisms have been proposed to explain how biodiversity enhances ecosystem processes. Firstly, local deterministic processes such as niche differentiation and facilitation may raise the productivity of the community above what would be

expected by sum of individual species grown alone (Loreau 2001). Secondly, stochastic processes of community assembly coupled with local dominance of one or more highly productive species may result in higher diversity plots having a higher probability of containing productive species, and thus a trend of increasing productivity with diversity. (cited in Loreau 2001).

As well as enhancing overall primary production, higher biodiversity may have impacts on the growth patterns and allometry of individual trees. This idea has not been previously investigated in the literature (to the best of our knowledge), but may be an interesting avenue of investigation.

1.4 The Sardinilla Carbon Project

The Sardinilla Carbon Project is a long-term research initiative led by McGill University and the Smisthonian Tropical Research Institute, with contributions from scientists from Panama, Canada, Germany and the United States. Established in 2001 under the direction of Dr. Catherine Potvin of McGill University, the project has converted abandoned pastureland into an experimental plantation containing 6 native hardwood species. One of the primary objectives of the project is to study the effects of biodiversity and land use change on ecosystem productivity and carbon sequestration. More specifically, the Sardinilla Carbon Project seeks to determine: a) how the transition in land use from grazed pasture to tree plantation affects ecosystem fluxes of carbon, and b) how community richness and identity of tree species affect carbon accumulation and cycling (Potvin, 2003).

1.5 Objectives of our Study:

Our study had two principal objectives. Firstly, we sought to develop species-specific allometric models for the six species in the Sardinilla plantation capable of predicting above ground biomass (AGB) from easily measurable and non-destructive parameters. These equations will be useful to our host organization (STRI/McGill) in quantifying plot-level biomass accumulation in the Sardinilla experimental plantation. The use of these regression models will also allow for rapid and non-destructive

estimates of biomass for any researchers working with these particular species in the future.

Secondly we sought to study the effect of increasing biodiversity on allometric relationships. This investigation could have both theoretical and practical applications in the fields of forest ecology and management. Our results may contribute to the growing body of literature attempting to disentangle the relationship between biodiversity and ecosystem function in forest ecosystems. Also, our findings may indicate whether biodiversity is a parameter that should be taken into account when deriving allometric equations for plantation biomass estimates.

In general, all the data generated in this investigation may contribute to improved biomass estimates within tropical plantations and a better understanding of the carbon sequestration potential associated with reforestation. Quantitative data on carbon sequestration rates of specific native species in tropical plantations may also have important applications for the carbon credit system.

Our product for our supervisor will be comprised of: biomass data and specific leaf area values for 150 trees in the Sardinilla plantation, and allometric equations for each of the six species in the plantation.

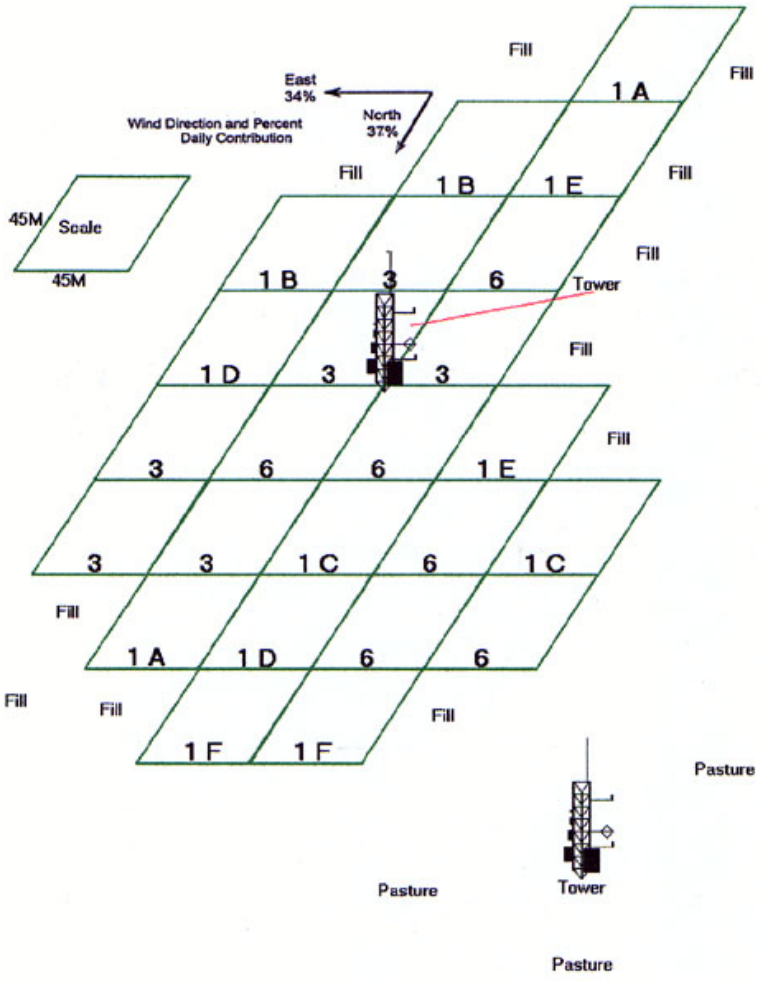
METHODS

2.1 Study Site

The Sardinilla Carbon Project plantation is based in Sardinilla (9o19'30"N, 79o38'00"W), a small village in the region of Buena Vista, Panama. Six native tree species were selected for planting, including 2 pioneers (*Luehea seemanii* and *Cordia alliodora)*, 2 light-intermediate species (*Anacardium excelsum* and *Hura crepitans)* and 2 shade tolerant species (*Cedrela odorata* and *Tabebuia rosea).* The plantation was divided into 24 plots of equal size (Fig. 1). Twelve plots (2 for each species) are monocultures, six plots contain different combinations of 3 tree species, and 6 plots contain all tree species. Undergrowth is cleared annually to eliminate other competing vegetation and facilitate work within the plantation. Each plot was randomly distributed

in order to reduce bias caused by differences in soil conditions. Plots are square-shaped and hold 225 trees each, planted at 3 m spacing. For data analysis purposes, each plot was divided into 4 sub-plots; each holding 56 trees. The trees were planted in 2001 and will be 5 years old as of this summer (2006).

Fig. 1: Plantation design for Sardinilla Carbon Project



Plots 1A through 1F are monocultures, plots labeled 3 are 3-species combinations, and plots labeled 6 are 6-species combinations (Potvin, date)

2.2 Determination of Biomass:

2.2.1 Sampling Protocol:

We sampled 10 trees per species per treatment (monoculture, 3-species combination, or 6-species combination) to determine the effects of species and treatment on biomass accumulation. Our objective was that this sample of 10 individuals be representative of the size range in the species-treatment group of interest. Therefore, within each species-treatment group, we ranked all individuals by height, and divided them into 3 equal size classes (small, medium and large). Of the 10 individuals to be sampled from each species-treatment group, 3 were chosen randomly from the small size class, 3 from the medium size class, 3 from the large size class, and 1 chosen randomly from the entire data set. On the field, not all size categories hold the same number of trees, our method is not completely random. Instead, it is called selected random and is commonly used for its capacity to undergo statistical analysis.

This protocol deferred slightly for *Cordia alliodora* (Ca), which has shown very poor growth and survival across all treatments. To avoid reducing the Ca stock more than absolutely necessary, we sampled only 5 individuals from this species. All Ca across the entire plantation were ranked by height, and divided into 5 size classes. We randomly chose 1 Ca individual to sample per size class from the entire plantation, regardless of treatment.

The following protocols will be followed to randomly select trees for each of the three treatments:

2.2.1.1 Monoculture:

We ranked all the trees of one species by height over the entire treatment (2 plots). We divided the trees into 3 equal height classes (small, medium, large), and pick 3 trees at random from each size class, respecting the following two restrictions. Firstly, trees cannot come from the same subplot, unless all subplots have been filled. Secondly, within a size class, all 3 trees cannot come from the same plot. A tenth tree was selected at random from one of the size classes (sampled size class was determined randomly by

rolling a die). Within size classes, individual trees were randomly selected from an Excel spreadsheet using a random number generator (www.random.org) to select their row number.

Figure 1: Sampling Protocol for Monoculture Treatment

Plot	Trees to sample	Size Class
Hc1, Hc2	10 Hc	3 small, 3 medium, 3 large, 1 random (large)
Cm1, Cm2	10 Cm	3 small, 3 medium, 3 large, 1 random (medium)
Tr1, Tr2	10 Tr	3 small, 3 medium, 3 large, 1 random (medium)
Ls1, Ls2	10 Ls	3 small, 3 medium, 3 large, 1 random (large)
Ae1, Ae2	10 Ae	3 small, 3 medium, 3 large, 1 random (small)

2.2.1.2 Three Species Plots:

We ranked all the trees of one species by height over the entire treatment (3 plots). We divided the trees into 3 equal height classes (small, medium, large). Within each plot, we randomly selected 1 tree from each of 3 size classes, with the restriction that no two trees could come from the same subplot. A tenth tree was selected at random from one of the plots (plot and size class were selected randomly by rolling a die). Within plots and size classes, individual trees were randomly selected from an Excel spreadsheet using a random number generator (www.random.org) to select their row number.

Figure 2: Sampling Protocol for 3 Species Plots

Plot	Species	Trees to Sample
T1	Ca	--------
	Cm	1 small, 1 medium, 1 large, 1 random (medium)
	Hc (3)	1 small, 1 medium, 1 large
T2	Ls	1 small, 1 medium, 1 large, 1 random (small)
	Ae	1 small, 1 medium, 1 large
	Tr	1 small, 1 medium, 1 large, 1 random (medium)
T3	Ls	1 small, 1 medium, 1 large
	Cm	1 small, 1 medium, 1 large
	Ae	1 small, 1 medium, 1 large
T4	Ls	1 small, 1 medium, 1 large
	Hc (3)	1 small, 1 medium, 1 large
	Cm	1 small, 1 medium, 1 large
T5	Ca	----------
	Hc (4)	1 small, 1 medium, 1 large, 1 random (medium)

T6	Tr	1 small, 1 medium, 1 large
	Ca	--------
	Ae	1 small, 1 medium, 1 large, 1 random (medium)
	Tr	1 small, 1 medium, 1 large

2.2.1.1 Six Species Plots:

For each species, the 10 individuals to be sampled were chosen from across the 6 plots containing 6-species mixtures. We randomly determined which plots would contain 1 sample, and which would contain 2, for a total of 2 + 2 + 2 + 2 + 1 + 1 = 10. We randomly allocated 3 small, 3 medium 3 large, and 1 random tree throughout the 6 plots. We then ranked all trees of 1 species by height over entire treatment (6 plots), and divided trees into 3 equal height classes (small, medium, large). Within each plot, we randomly selected 1 or 2 trees from the appropriate size class, with the restriction that no two trees could come from the same subplot. Within plots and size classes, individual trees were randomly selected from an Excel spreadsheet using a random number generator (www.random.org) to select their row number.

Figure 3: Sampling Protocol for 6 Species Plots

Plot	**Species**	**Trees to Sample**
A1	Hc	S
	Cm	M
	Tr	S
	Ls	M
	Ae	M
	Ca	-----
A2	Hc	M, S
	Cm	M, S
	Tr	M, L
	Ls	S
	Ae	S
	Ca	----
A3	Hc	S
	Cm	L, S
	Tr	M, L
	Ls	L, L
	Ae	S, M
	Ca	----
A4	Hc	L, S
	Cm	M, L

	Tr	M, L
	Ls	S, M
	Ae	L, L
	Ca	----
A5	Hc	M, L
	Cm	L
	Tr	S
	Ls	S, L
	Ae	L, S
	Ca	---
A6	Hc	M, L
	Cm	S, M
	Tr	S, S
	Ls	M, S
	Ae	M, L
	Ca	----

Figure 4: Trees to Cut by Species and Treatment:

Species	Treatment	Small	Medium	Large
Hc	Monoculture	Hc2-3 9-11 Hc1-4 4-15 Hc2-2 11-1	Hc2-1 2-6 Hc2-1 2-9, Hc1-1 1-6	Hc1-3 11-15 Hc1-3 15-13 Hc1-2 9-6 Hc1-2 14-5
Hc	3-species	T4-4 5-8 T5-3 9-9 T1-4 7-12	T4-3 14-11 T1-3 10-13 T5-1 10-13 T5-2 12-6	T5-4 6-12 T4-2 14-2 T1-2 8-4
Hc	6-species	A1-4 4-9 A2-3 12-8 A3-2 14-1 A4-4 1-9	A2-4 2-10 A5-2 10-1 A6-3 12-9	A4-1 3-5 A5-1 7-4 A6-1 2-1
Cm	Monoculture	Cm2-4 3-5 9-1 Cm2-2 Cm1-2 14-3	Cm1-4 6-14 Cm1-3 16-12 Cm2-3 14-12 Cm2-1 4-2	Cm2-2 13-5 Cm1-1 3-8 Cm2-3 10-15
Cm	3-species	T1-3 9-12 T3-4 7-10 T4-1 5-6	T1-4 1-10 T1-2 10-7 T3-2 10-4 T4-4 6-10	T1-1 3-6 T3-1 7-1 T4-3 13-11
Cm	6-species	A2-2 15-7 A3-1 6-7 A6-3 14-9	A1-1 2-7 4-8 A2-4= A2-4 5-8 was cut instead:exclude A4-1 5-3 A6-4 2-9	A3-3 8-15 A4-2 15-1 A5-1 4-3

Tr	Monoculture	Tr1-2 9-7 Tr2-3 13-15 Tr1-4 4-11	Tr2-2 8-4 Tr2-1 4-1 Tr1-1 7-1 Tr1-4 7-15	Tr2-4 1-8 Tr2-2 15-3 Tr1-3 14-14
Tr	3-species	T6-3 10-16 T5-2 12-2 T2-2 16-4	T5-3 15-11 T2-1 8-3 T6-4 4-13 T2-3 16-10	T6-2 10-4 T2-4 8-9 T5-1 1-6
Tr	6-species	A1-2 12-2 A5-3 913, A6-3 14-8 A6-4 3-13	A2-3 10-13 A3-1 4-4 A4-1 1-4	A2-2 11-2 A3-4 1-3, A4-4 7-10
Ls	Monoculture	13-7 Ls2-2 Ls2-1 1-3 Ls1-2 11-3 Ls2-2 14-2	Ls1-2 13-3 Ls1-3 11-12 Ls2-3 9-12	Ls1-4 3-13 Ls1-1 4-4 Ls2-4 3-11
Ls	3-species	T2-2 13-2 T4-3 10-15 T3-4 7-11 T3-2 12-6	T2-1 8-4 T4-4 3-14 T3-3 15-12	T4-2 9-5 T3-1 7-2 T2-4 5-13
Ls	6-species	A2-3 15-9 A4-3 12-12 A5-4 14-9 A6-3 10-9	A1-1 2-3 A4-1 7-1 A6-1 6-1	A3-4 1-10 A3-1 1-4 A5-1 7-8
Ae	Monoculture	Ae2-2 8-1 Ae1-1 5-7 Ae2-3 13-11 Ae2-1 5-4	Ae2-1 3-7 Ae1-4 1-12 Ae2-4 1-11	Ae1-3 14-9 Ae1-2 8-2 Ae2-2 13-2
Ae	3-species	T6-1 7-6 T3-3 16-15 T2-2 10-3	T6-4 4-9 T3-1 4-3 T2-1 7-6 T6-2 12-4	T2-4 5-14 T2-3 16-12 T3-2 11-2 (constraints)
Ae	6-species	A2-2 9-4 A3-3 15-13 A5-2 10-6	A1-4 3-15 A3-1 3-7 A6-1 7-1	A6-4 3-11 A4-4 6-13 A4-2 12-7 A5-1 4-6

Ca:

1st Height class: T6-4 4-8

2nd Height class: 2-9 Ca1-4

3rd Height class: 6-7 T1-1

4th Height class: 11-10 A4-3

5th Height class: 8-12 T5-3

2.2.2 Collection of woody debris prior to cut:

To avoid confusion between woody debris that is already in the plots and that left on the ground during our biomass sampling, we collected and weighed all large woody debris that was on the ground in every plot prior to the cut. Each plot was searched by a team of 6 people, each person walked in a straight line and collecting all visible woody debris (twigs, branches, trunks) belonging to the tree species in that plot. Leaf litter and litter from the undergrowth were excluded.

2.2.3 Tree-felling Protocol:

Each tree to be cut was marked ahead of time with spray paint and identified with a metal tag bearing its location and species code. Trees were cut at the base, as close to the ground as possible, using either a handsaw or chainsaw, depending on the trunk diameter. Large trees were lowered with ropes to avoid damaging other trees. If necessary, we also removed branches prior to cutting the tree to avoid hitting neighbouring trees. When this was done, branches were properly separated by height class before being removed (see below).

2.2.4 Measurement Protocol:

2.2.4.1 Trunks and branches:

For trees with multiple stems, we considered the stem with largest diameter at breast height (DBH) to be the primary trunk. We measured the bole length of the primary trunk, defined as the distance from the ground to the first major branching point. We measured the distance between the lowest and highest branch of primary trunk and divided this distance into 3 equal parts. This was used to classify branches as low, middle, and high. We removed all branches from the primary trunk and separated them as low, middle and high. Using a 20kg capacity scale, we weighed separately: the primary trunk, the low branches of primary trunk, middle branches of primary trunk, high branches of primary trunk, secondary (tertiary, etc…) trunks, and branches of the secondary trunks (each secondary trunk has an associated mass of secondary branches). We took a sub-sample of 2 branches from each of the three height categories of the primary trunk. We weighed

these branches, remove all leaves, and then weighed again to determine the mean fresh weight of leaves.

2.2.4.2 Leaves

We were originally supposed to take a sample of 2 leaves from each portion of the cut trees (low, middle, high). We would then trace each fresh leaf on a piece of white paper, in order to calculate specific leaf area. However, there was an error made in the initial data collection (leaves were not traced when they were fresh), and so we re-collected leaves from a new set of trees, which were selected in the same manner as described above. In the case of trees with branches in only one height class, we would take a sample of 6 leaves from that one class. Once drawn, we stored each leaf in a separate, labeled page of an exercise book. Leaves were dried in a drying oven and reweighed using a Salter-AND EK 12 kg to determine dry weights.

The only difference in selection protocol was that the tenth random tree was from the same plot and height class as the original set of selected trees (rather than randomly selected by a die), to make the two data sets as comparable as possible.

Figure 5: Trees From Which to Sample Fresh Leaves for Specific Leaf Area:

Species	Treatment	Small	Medium	Large
Hc	Monoculture	Hc2 3 11-10 Hc2 2 10-4 Hc1 2 13-1	Hc1 4 6-8 Hc2 1 6-1 Hc2 4 8-15	Hc1 3 14-8 Hc1 3 12-15 Hc1 3 15-15 Hc1 3 15-12
Hc	3-species	T1-4 2-11 T4-1 3-6 T5-3 11-11	T1-4 3-12 T4-4 7-13 T5-3 8-5 T5-2 8-2	T1-3 10-15 T4-2 13-1 Dead T5-3 11-14
Hc	6-species	A1 2 12-7 A2 4 7-15 A3 1 5-4 A4 4 4-12	A6 4 2-13 A3 4 3-13 A5 1 4-1	A4 3 14-4 A4 1 7-3 A4 3 12-8 (forced to take tallest from medium category)
Cm	Monoculture	Cm2 4 2-9 Cm1 4 6-15	Cm2 1 3-1 Cm1 2 13-4	Cm1 3 9-11 Cm2 3 13-13

		Cm2 2 13-3	Cm2 2 11-4 Cm1 1 4-5	Cm1 1 7-5
Cm	3-species	T1-2 12-3 T3-2 12-5 T4-1 3-7	T1-4 2-8 T1-3 8-11 T3-1 5-1 (constraint) T4-1 3-7	T1-1 3-3 T3-1 6-2 T4-2 13-2
Cm	6-species	A2-3 11-15 A3-1 1-2 (no leaves, no alternative) A6-2 9-2	A4-3 10-8 A6-4 6-11 A1-4 4-11 A2-2 15-1	A3-1 4-5 A4-3 19-15 A5-2 9-2
Tr	Monoculture	Tr2 2 9-1 Tr1 3 10-11 Tr2 4 6-14	Tr2 1 7-1 Tr1 4 2-9 Tr2 4 4-15 Tr1 2 12-6	Tr2 3 8-10 Tr1 1 2-1 Tr1 2 11-8
Tr	3-species	T2-4 2-9 T5-3 13-9 T6-4 7-10	T2-3 9-8 T2-1 4-7 T5-1 3-2 T6-2 14-3	T2-2 13-4 T5-2 11-4 T5-4 4-12 (no large in T6)
Tr	6-species	A1 2 11-3 A5 3 14-12 A6 2 14-2 A6 4 6-10	A3 1 7-7 A4 2 11-2 A2 1 3-6	A3 4 3-15 A4 2 10-7 A6 4 7-15
Ls	Monoculture	Ls2 1 3-1 Ls2 2 15-4 Ls1 3 15-12	Ls1 4 6-10 Ls1 2 9-3 Ls2 3 10-9	Ls1 1 2-3 Ls 1 2 14-5 Ls2 4 2-14 Ls2 4 3-14 (no choice)
Ls	3-species	T2-1 2-1 T3-3 16-8 T3-4 4-8 T4-4 2-10	T2-2 12-3 T3-2 16-2 T4-3 8-13	T2-3 10-8 T3-1 4-2 T4-2 13-6
Ls	6-species	----	----	---
Ae	Monoculture	Ae1 2 9-5 Ae2 3 10-13 Ae1 4 3-9 Ae2 4 3-10	Ae1 3 8-10 Ae2 3 15-9 Ae1 4 1-12 (tree cut)	Ae2 1 3-2 Ae1 1 7-2 Ae2 2 15-4
Ae	3-species	T2-1 4-3 T3-4 8-14 T6-1 2-5	T2-3 13-12 T3-1 6-4 T6-3 9-10 T6-1 3-7	T2-2 13-6 T3-2 15-1 T3-1 8-2 (no large in T6)
Ae	6-species	----	---	---

Ca:

8-6 Ca1 2

12-1 T1 2

14-13 A 4 3

10-11 T5 3

2-4 A 3 1

2.2.4.3 Trunk segments:

We took small segments of the following: bottom of primary trunk, top of primary trunk, low branches, middle branches, high branches. We weighed each trunk segment using a Salter-AND EK 12 kg scale to determine its fresh weight. We then stored each segment in a separate labeled paper bag, to be dried in a drying oven and reweighed to determine its dry weight.

2.3 Data Analysis:

2.3.1 Biomass Calculation:

From the data collected, we were able to calculate the dry weight of each harvested tree. Although branches were weighed with their leaves in the field for simplicity, biomass measurements typically include permanent woody tissues only. Therefore, the fresh weight of all branches without leaves was estimated based on ratios calculated from two sample branches that were weighed with and without leaves from each tree. All fresh weights were then converted to dry weights, taking into consideration the fact that water concentrations differ between branches and trunks. Dry to fresh weight ratios were calculated for trunks and the different height categories of branches, based on the wood segments taken from these tissues. Multiplying these ratios with the fresh weights obtained on the field gave us the dry weight of trunks, low branches, medium branches and high branches. For trunks, we used a dry to fresh weight ratio that was calculated by averaging the ratios found from the top and bottom trunk segments. Dry weights of each structural component were then summed to calculate the total dry weight of the tree.

2.3.2 Independent Variables:

As mentioned above, diameter at breast height (DBH), height, and specific wood density have been found to be the most important predictors of biomass (Chave et al 2005). In our study, we considered these three parameters, as well as two new ones: basal diameter and DBH of all stems. The latter measurement was important because many of the trees in the plantation had multiple stems, and so two measures of diameter were considered: diameter of the largest stem ("DBH"), and the sum of diameters of all stems ("DBHall").

Basal diameter (in cm) was measured as the diameter of the principal stem at 10 cm above the ground, and height (in m) as the distance from the ground to the crown along the main stem. DBH measurements were taken at a height of 1.3m from the ground on all stems. Wood specific densities (SD) for the species under consideration were obtained from an online databank (Wood Density Database). Wood density is typically considered as dry weight over fresh volume (g/cm^3). DBH and height measurements were taken by the local managers of the plantation at the same time as our study.

2.3.3 Regression analysis and model construction:

Before proceeding with regression analysis, the data were examined to ensure that the assumptions of regression analysis would not be violated. Pearson correlation matrices were generated to test for correlations between independent variables, i.e. multicollinearity. If substantial correlations were found between independent variables, multiple linear regression analysis was not attempted; as multicollinearity makes conclusions drawn from such analyzes unreliable (Zar 1999). Other authors have circumvented the problem of multicollinearity by using compound variables with a single coefficient (e.g. Nelson et al. 1999), and this was attempted when necessary. Scatter plots were generated to test qualitatively for the type of functional relationship between biomass and each of the independent variables, and to check for heteroscedascity in Y values (variation in variance of Y values with increasing value of X). When necessary,

data were log-transformed (Y' = lnY) to linearize the relationship or minimize the heteroscedascity in Y values.

Various simple linear regressions were systemically attempted, starting with the parameter most highly correlated with biomass, and increasing in complexity by incorporating other variables. Models were compared and evaluated based on the coefficient of determination (r^2 = regression SS/total SS). The significance of each regression was tested by analysis of variance testing, and the F ratio (F = regression MS/residual MS) and p value were reported. The significance level, α, was set at 0.05 for all analyzes. All statistical analyzes were performed with SYSTAT 10.2.

2.3.4 Determining Biodiversity Effects:

To examine the effects on biodiversity on carbon sequestration rates and patterns, regressions were compared between treatments within each species. The three most simple regressions (ln(biomass) as a function of ln(height), ln(dbh), and ln(basal diameter) respectively) were selected for this analysis. The slopes of these regressions were compared by analysis of covariance. We tested the null hypothesis $H_o = \beta_1 = \beta_3 = \beta_6$, where β_1 is the slope of the regression for the monoculture treatment, β_3 is the slope of the regression for the 3-species treatment, and β_6 is the slope of the regression for the 6-species treatment. This hypothesis was tested by calculating the F statistic, using the General Linear Model function in SYSTAT. Differences between pairs of treatments were tested for using the Bonferroni multiple comparison test in SYSTAT, which is considered to be more powerful than the Tukey test for a small number of pairs.

RESULTS

3.1 Species-specific regression models

In this section, we report our results for the construction of allometric equations that best predict values of above ground biomass (AGB) based upon easily measurable and non-destructive parameters. Parameters used are: DBH (diameter of largest trunk at 1.3 m from the ground), Dall (sum of the diameter of all trunks at 1.3 m), Basal (diameter at ground level) and height. We present our models and compare them to the models most commonly used in the literature. It should be noted, however, that models borrowed from other authors were developed using data from mature natural forests.

3.1.1 Tabebuia rosea (Tr)

As shown in Table 2, the parameters with the strongest correlation to tree biomass were height (0.824) and DBH (0.702). Basal diameter had a slightly weaker correlation to biomass. It was still used however to elaborate our model for estimation of biomass (Table 1). The higher precision of model 2 in comparison to model 1 is due to the exclusion of data that were considered as outliers by the computer software (SYSTAT). Notice how weakly models developed by Brown et *al.* (1989), Nelson et *al.* (1999) and Overman et *al.* (1999) fit our data.

Table 1.

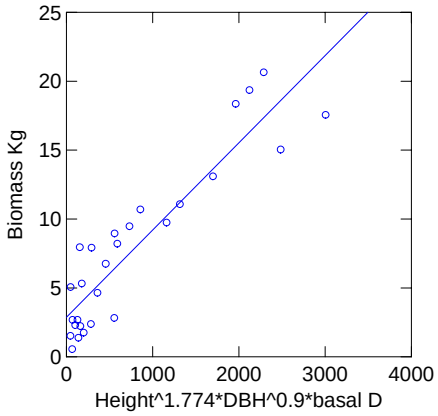
Regression models for estimation of above-ground biomass for *Tabebuia rosea*. Equations were developed based upon 30 sample individuals from a 5-year old tropical plantation. Models 2,3 and 4 were constructed by excluding detected outliers.

Regression model	**Coefficient Symbol**	**Coefficient value**	**Standard error**	**r^2**	**Significance level of F-ratio**
1) $DW = c + \alpha\ (Height^{1.774} \times DBH^{0.9} \times Basal\ D)$	α	0.005	0.001	0.716	<0.0005
	c	3.153	0.805		
2) $DW = c + \alpha\ (Height^{1.774} \times DBH^{0.9} \times Basal\ D)$	α	0.006	0.001	0.837	<0.0005
	c	2.874	0.636		
3) $DW = c \times DBH^{\alpha}$	α	1.128	0.294	0.371	0.001
(Brown et *al.* 1989, Nelson et *al.* 1999, Overman et *al.* 1994	c	0.044	0.507		
4) $DW = c\ (DBH^2 \times Height)^{\alpha}$	α	0.845	0.096	0.475	<0.0005
(Brown et *al.* 1989, Nelson et *al.* 1999)	c	0.328	0.471		

Table 2. Correlation coefficients between biomass and easily measurable parameters of *Tabebuia rosea*

	BIOMASS	HEIGHT	DALL	DBH	BASAL
BIOMASS	1.000				
HEIGHT	0.824	1.000			
DALL	0.673	0.710	1.000		
DBH	0.702	0.781	0.735	1.000	
BASAL	0.690	0.583	0.455	0.427	1.000

Figure 1. Linear regression of data from *Tabebuia rosea* used to construct the best-fitting AGB model.



3.1.2 Hura Crepitans

The models for estimating biomass proposed by Brown et *al.* (1989) and Nelson et *al.* (1999) most accurately represented our data for dry weight of *Hura crepitans*. No outliers were reported while testing models 1 and 2 (Table 3) on our data for biomass, meaning that the dry weight values, DBH and height of *Hura Crepitans* tightly fit the regression line (Fig. 2). Before log-transformation, the scatter-plot for biomass in function of DBH^2 x Height had the shape of a power function. The log transformation provided the linear curve needed to test for regression (Fig. 2). The model gained in precision when height was considered. Adding the total diameter of trunks at 1.3 m (Dall) did not increase the accuracy of the model and integrating basal diameter actually led to a slight reduction in accuracy. The fact that the most precise models originate from height and DBH does not coincide with what one would expect from the calculated coefficients of correlation (Table 4). Indeed, of the 4 parameters, basal diameter (basal) and diameter of all branches (dall) had the best correlations to biomass.

Table 3.

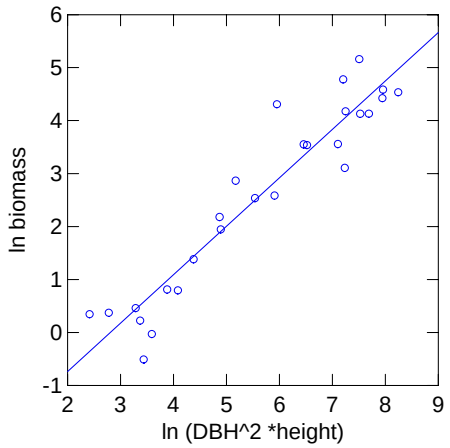
Regression models for estimation of aboveground biomass of *Hura Crepitans*. Equations are developed based upon 30 sample individuals from a 5-year old tropical plantation.

Regression model	**Coefficient Symbol**	**Coefficient value**	**Standard error**	r^2	**Significance level of F-ratio**
1) $DW = c \times DBH^{\alpha}$	α	2.478	0.191	0.871	<0.0005
(Brown et *al.* 1989, Nelson et *al.* 1999, Overman et *al*. 1994)	c	2.456	0.408		
2) $DW = c \times (DBH^2 \times Height)^{\alpha}$	α	0.915	0.061	0.899	<0.0005
(Brown et *al.* 1989, Nelson et *al.* 1999)	c	2.568	0.360		

Table 4. Correlation coefficients between biomass and easily measurable parameters of *Hura Crepitans*

	BIOMASS	HEIGHT	DALL	DBH	BASAL
BIOMASS	1.000				
HEIGHT	0.754	1.000			
DALL	0.871	0.752	1.000		
DBH	0.777	0.824	0.837	1.000	
BASAL	0.811	0.818	0.825	0.880	1.000

Figure 2. Linear regression of transformed data from *Hura crepitans* used to construct the best-fitting AGB model.



3.1.3 Cedrela odorata

Of the 6 species studied in the Sardinilla project, Cm had the weakest models for the prediction of AGB. Regressions for ln(biomass) in function of ln(basal diameter) held 6 outliers. Two of these (T3-4 7-10 and T1-2 10-7) were excluded from all 4 models because it was obvious that they originated from field mistakes. Then, the 2 most important outliers (A6-4 2-9) and (Cm1-1 3-5), were not considered in models 2, 3 and 4 to see if their exclusion could significantly raise the value of r^2. Unfortunately, extracting outliers from regression data sets reduces the number of individuals used to test for regression, meaning that the results may be less representative of the studied population. The model that best predicted above ground biomass used basal diameter as a parameter (Table 5). Basal diameter also had the highest correlation coefficient to biomass (Table 6)

Table 5.

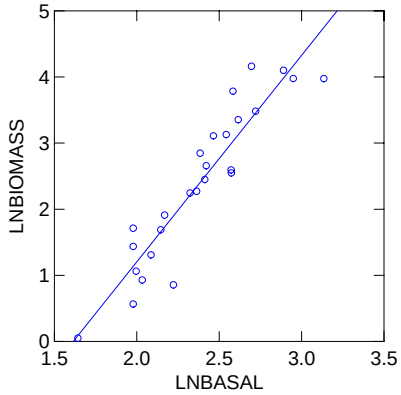
Regression models for estimation of aboveground biomass of *Cedrela odorata*. Equations were developed based upon 30 sample individuals from a 5-year old tropical plantation. Models 2, 3 and 4 were constructed by excluding detected outliers.

Regression model	**Coefficient Symbol**	**Coefficient value**	**Standard error**	r^2	**Significance level of F-ratio**
1) $DW = c \times (basal)^{\alpha}$	α	2.689	0.406	0.627	<0.0005
	c	3.967	0.971		
2) $DW = c \times (basal)^{\alpha}$	α	3.123	0.254	0.863	<0.0005
	c	5.041	0.611		
3) $DW = c \times DBH^{\alpha}$	α	1.783	0.235	0.697	<0.0005
(Brown et *al.* 1989, Nelson et *al.* 1999, Overman et *al.* 1994)	c	0.948	0.453		
4) $DW = c \times (DBH^2 \times Height)^{\alpha}$	α	0.607	0.079	0.701	<0.0005
(Brown et *al.* 1989, Nelson et *al.* 1999)	c	0.955	0.449		

Table 6. Corellation coefficients between biomass and easely measurable parameters of Cedrela odorata

	BIOMASS	HEIGHT	DALL	DBH	BASAL
BIOMASS	1.000				
HEIGHT	0.697	1.000			
DALL	0.718	0.753	1.000		
DBH	0.704	0.940	0.708	1.000	
BASAL	0.777	0.855	0.823	0.854	1.000

Figure 3. Linear regression of transformed data from *Cedrela odorata* used for best-fit AGB model.



3.1.4 Luehea seemannii

DBH was a poor predictor of aboveground biomass for Ls. As can be seen in Table 7, the model developed by previous ecologists only has an r^2 value of 0.291. As we have already seen for *Hura crepitans*, the parameters used in the regression model that best fits the biomass data are not necessarily the ones with the highest coefficients of correlation to dry weight values (Table 8). Of the 4 tree parameters studied, tree height actually has the lowest coefficient of correlation to biomass. For model 1 (Table 7), the computer software did not detect any outliers.

Table 7.

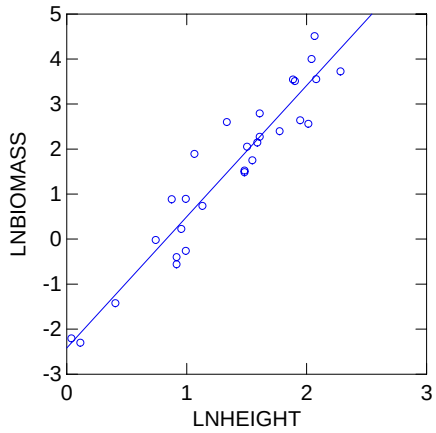
Regression models for estimation of aboveground biomass of *Luehea seemanii*. Equations were developed based upon 30 sample individuals from a 5-year old tropical plantation.

Regression model	**Coefficient Symbol**	**Coefficient value**	**Standard error**	**r^2**	**Significance level of F-ratio**
1) $DW = c \times (Height^{\alpha})$	α	2.917	0.951	0.904	<0.0005
	c	-2.42	0.183		
2) $DW = c \times DBH^{\alpha}$	α	0.912	0.280	0.281	0.001
(Brown et *al.* 1989, Nelson et *al.* 1999, Overman et *al.* 1994)	c	0.085	0.533		
3) $DW = c \times (DBH^2 \times Height)^{\alpha}$	α	0.999	0.100	0.786	<0.0005
(Brown et *al.* 1989, Nelson et *al.* 1999)	c	2.609	0.445		

Table 8. Corellation coefficients between biomass and easely measurable parameters of *Luehea seemannii*.

	BIOMASS	HEIGHT	DALL	DBH	BASAL
BIOMASS	1.000				
HEIGHT	0.760	1.000			
DALL	0.851	0.895	1.000		
DBH	0.774	0.921	0.896	1.000	
BASAL	0.798	0.871	0.905	0.862	1.000

Figure 4. Linear regression of transformed data from *Luehea seemannii* used for best-fit AGB model.



3.1.5 Anacardium Exclesum

Models for the estimation of biomass from tree parameters from Brown et *al.*, Nelson et *al.* and Overman et *al.* were very similar to those we developed (Table 9). DBH and height were used as predictors of AGB in both cases. The difference in r^2 value from models 1-2 to models 3-4 (Table 9) is explained by the exclusion of an outlier when testing models 1 and 2 (the outlier was Ae 2-3 13-11). When testing models 3 and 4, no outliers were reported. The similarity in r^2 values between model 1 and 2 suggests that the use of exponents to modify the parameters of DBH and height brings no further accuracy to the models. Models for predicting above ground biomass (AGB) for *Anacardium Exclesum* were the most accurate of the 5 species studied for which equations were based upon 30 individuals (i.e. Hc. Tr, Ls, Cm and Ae). The coefficients of correlation between easily measurable parameters and biomass values were also the highest for Ae out of the 5 species with 30 sampled trees (Table 9). Remember that for reasons of low survival rate, Ca had only 5 trees sampled over the entire plantation.

Table 9.

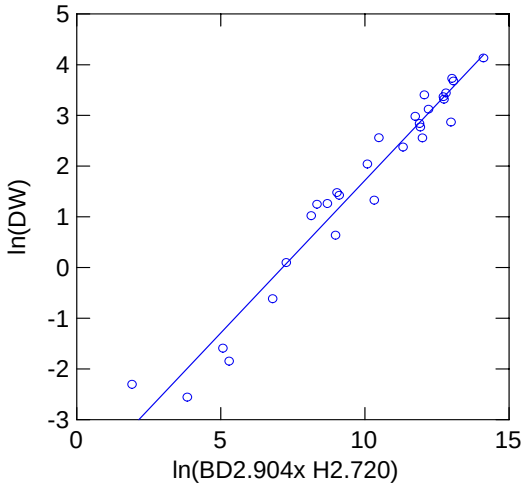
Regression models for estimation of aboveground biomass of *Anacardium Exclesum*. Equations were developed based upon 30 sample individuals from a 5-year-old tropical plantation. Model 1 and 2 were constructed by excluding 1 detected outlier (AE 2-3 13-11).

Regression model	**Coefficient Symbol**	**Coefficient value**	**Standard error**	**r^2**	**Significance level of F-ratio**
1) $DW = c \times (BDH^{2.904} \times Height^{2..720})^{\alpha}$	α	0.602	0.025	0.957	<0.0005
	c	-4.296	0.255		
2) $DW = c \times (BDH \times Height)^{\alpha}$	α	1.691	0.070	0.956	<0.0005
	c	-4.246	0.257		
3) $DW = c \times DBH^{\alpha}$	α	2.857	0.357	0.695	<0.0005
(Brown et *al.* 1989, Nelson et *al.* 1999, Overman et *al.* 1994)	c	2.986	0.612		
4) $DW = c \times (DBH^2 \times Height)^{\alpha}$	α	0.988	0.104	0.763	<0.0005
(Brown et al. 1989, Nelson et al. 1999)	c	2.825	0.503		

Table 10 . Correlation coefficients between biomass and easily measurable parameters of *Anacardium Exclesum.*

	BIOMASS	HEIGHT	DALL	DBH	BASAL D
BIOMASS	1.000				
HEIGHT	0.825	1.000			
DALL	0.836	0.779	1.000		
DBH	0.848	0.926	0.819	1.000	
BASAL D	0.878	0.865	0.846	0.887	1.000

Figure 5. Linear regression of transformed data from *Anacardium exclesum* used for best-fit model of AGB.



3.1.6 Cordia Alliodora (Ca)

Two outliers were reported for model 3 (Table 11). Due to high mortality rates throughout the plantation, we were only able to harvest 5 individuals for this species. Removing any outlier from the analysis would have decreased the sample pool by a ratio much too large to be justifiable. However, there was no need to extract outliers as all models from Table 11 have the highest r^2 values of our project. Although the significance level of the F-ratio is significant, the small size of the sample pool from which models 1, 2 and 3 (Table 11) were constructed may limit the level to which these models truly represent AGB of all trees of Ca. Including height as a parameter to model 3 reduced its accuracy in comparison to model 1 and 2 (Table 11). Also it was for model 3 that outliers were found. This suggests that data for height for Ca was probably less correlated with biomass than was data for DBH. Indeed, as shown in table 12, the coefficient of correlation between AGB and DBH was 0.992 while the coefficient of correlation between AGB and height was 0.986.

Table 11.

Regression models for estimation of aboveground biomass of *Cordia Alliodora*. Equations were developed based upon 5 sample individuals from a 5-year old tropical plantation. No outliers were excluded due to small sample size.

Regression model	**Coefficient Symbol**	**Coefficient value**	**Standard error**	**r^2**	**Significance level of F-ratio**
1) $DW = c + \alpha\ BDH^{1.633}$	α	0.335	0.014	0.995	<0.0005
	c	0.537	0.472		
2) $DW = c \times DBH^{\alpha}$	α	1.633	0.107	0.987	0.001
(Brown et *al*. 1989, Nelson et *al*. 1999, Overman et *al*. 1994)	c	0.044	0.507		
3) $DW = c \times (DBH^2 \times Height)^{\alpha}$	α	0.561	0.056	0.970	<0.0005
(Brown et al. 1989, Nelson et al. 1999)	c	1.028	0.307		

Table 12. Correlation coefficients between biomass and easily measurable parameters of *Cordia Alliodora*.

	BIOMASS	HEIGHT	DALL	DBH	BASAL
BIOMASS	1.000				
HEIGHT	0.986	1.000			
DALL	0.956	0.962	1.000		
DBH	0.992	0.975	0.913	1.000	
BASAL	0.994	0.976	0.975	0.974	1.000

Figure 6. Linear regression data from Cordia Alliodora (Ca) used for best-fit model of AGB.

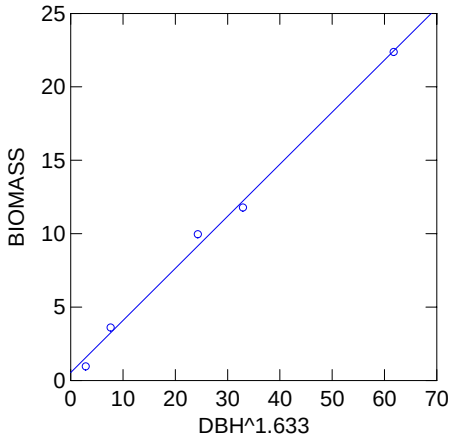


Table 13: Summary of Best Allometric Models for each Species

Regression model	Coefficient Symbol	Coefficient value	Standard error	r^2	Significance level of F-ratio
Tabebuia rosea					
$DW = c + \alpha (Height^{1.774} \times DBH^{0.9} \times Basal\ D)$	α	0.006	0.001	**0.837**	<0.0005
	C	2.874	0.636		
Hura Crepitans					
$DW = c \times (DBH^{2} \times Height)^{\alpha}$	α	0.915	0.061	**0.899**	<0.0005
	C	2.568	0.360		
Cedrela odorata					
$DW = c \times (basal)^{\alpha}$	α	3.123	0.254	**0.863**	<0.0005
	C	5.041	0.611		
Luehea seemannii					
$Dw = (Height^{\alpha}) \times c$	α	2.917	0.951	**0.904**	<0.0005
	C	-2.42	0.183		
Anacardium Exclesum					
$DW = c \times (BDH^{2.904} \times Height^{2..720})^{\alpha}$	α	0.602	0.025	**0.957**	<0.0005
	C	-4.296	0.255		
Cordia Alliodora					
$DW = c + \alpha \times BDH^{1.633}$	α	0.335	0.014	**0.995**	<0.0005
	C	0.537	0.472		

3.2 Effect of Biodiversity on Allometric Relationships

3.2.1 Tabebuia rosea:

For *Tabebuia rosea*, there were no significant differences in regression slopes between treatments for the ln(height) function ($F=0.413$, $p=0.666$), the ln(dbh) function ($F = 1.612$, $p=0.220$), or for the ln(basal) function ($F = 0.040$, $p=0.961$).

3.2.2 Hura Crepitans:

For *Hura crepitans*, there were no significant differences in regression slopes between treatments for the ln(height) function (F=0.192, p =0.827), the ln(dbh) function (F = 1.693, p =0.205), or for the ln(basal) function (F = 0.848, p =0.441).

3.2.3 Cedrela odorata:

For *Cedrela odorata*, there were no significant differences in regression slopes between treatments for the ln(basal) function (F = 1.519, p =0.240). However, for the ln(height) function, treatments differed significantly (F = 10.276, p = 0.001). In this case, the monoculture regression was the steepest, followed by 6-species and then 3-species (Table 14, Fig.7). Differences were detected between 3-species and monoculture ($p < 0.0005$), but not between monoculture and 6-species (p = 0.106), or between 3-species and 6-species (p=0.095) (Table 15). Treatments also differed significantly for the ln(dbh) function (F= 7.536, p = 0.003). In this case, the monoculture regression was the steepest, followed by 6-species and then 3-species (Table 16, Fig.8). Differences were detected between 3-species and monoculture ($p < 0.002$), but not between monoculture and 6-species (p = 0.557), or between 3-species and 6-species (p=0.055) (Table 17).

Table 14: Comparing regressions across treatments for $\ln(DW) = \alpha \ln(H)$, for Cm

Treatment	Mono*	3-sp**	6-sp***
n	9	9	9
b	2.309	2.143	2.145
r^2 of regression	0.701	0.853	0.918

*1outlier excluded (Cm1-1 3-5)

**2 outliers excluded (T3-4 7-10, T1-2 10-7)

***1 outlier excluded (A6-4 2-9)

Table 15: Matrix of pairwise comparison probabilities (Bonferroni Test)

	3-sp	6-sp	mono
3-sp	1.000		
6-sp	0.095	1.000	
mono	0.000	0.106	1.000

Fig.7: ln(DW) = αln(H) plotted by treatment (Cm)

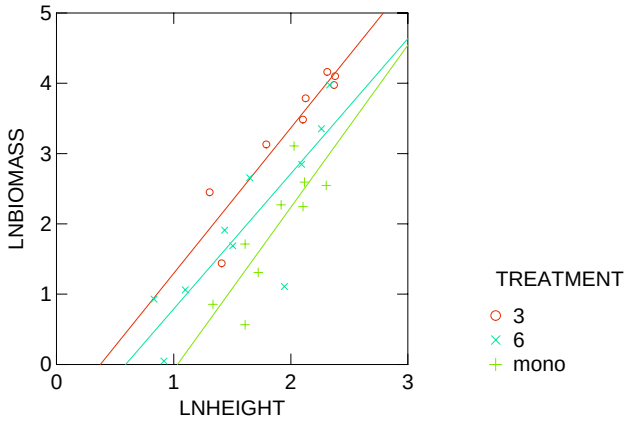


Table 16: Comparing regressions across treatments for ln(DW) = αln(DBH), for Cm

Treatment	Mono*	3-sp**	6-sp***
n	9	8	9
b	2.487	0.974	1.754
r^2 of regression	0.577	0.693	0.908

*1outlier excluded (Cm1-1 3-5)

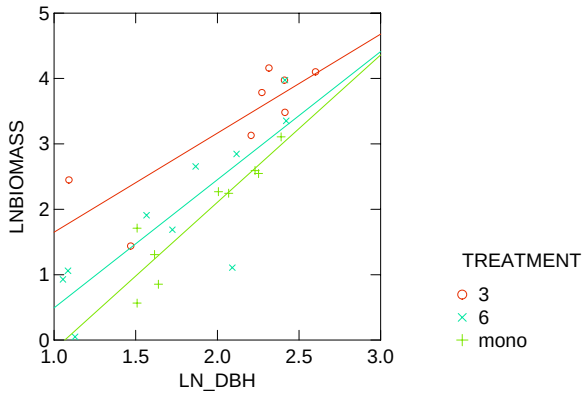
**2 outliers excluded (T3-4 7-10, T1-2 10-7)

***1 outlier excluded (A6-4 2-9)

Table 17: Matrix of pairwise comparison probabilities (Bonferroni Test)

	3-sp	6-sp	mono
3-sp	1.000		
6-sp	0.055	1.000	
mono	0.002	0.557	1.000

Fig. 8: ln(DW) = αln(DBH) plotted by treatment (Cm)



3.2.4 Luehea seemanii:

For *Luehea seemanii* , there were no significant differences in regression slopes between treatments for the ln(height) function (F=2.311, p =0.120), or for the ln(basal) function (F = 2.218, p =0.130). However, for the ln(dbh) function, treatments differed nearly significantly (F = 3.333, p = 0.052). In this case, the 6-species regression was the steepest, followed by 3-sp and then monoculture (Table 18, Fig.9). Differences were not significant between any of the combinations (Table 19).

Table 18: Comparing regressions across treatments for ln(DW) = αln(DBH), for Ls

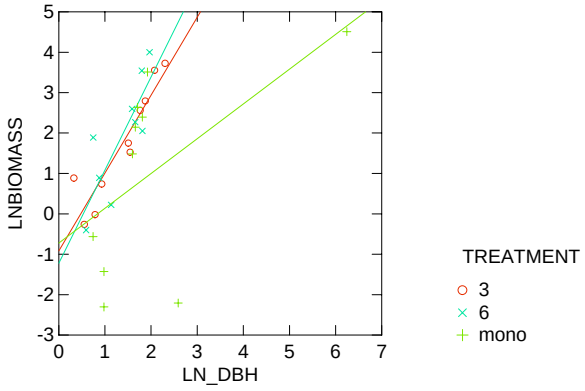
Treatment	Mono	3-sp	6-sp
n	10	10	9
b	0.860	1.928	2.304
r^2 of regression	0.306^o	0.857	0.678

^{o}result not significant

Table 19: Matrix of pairwise comparison probabilities (Bonferroni Test)

	3-sp	6-sp	mono
3-sp	1.000		
6-sp	1.000	1.000	
mono	0.128	0.080	1.000

Fig. 9: ln(DW) = αln(DBH) plotted by treatment (Ls)



3.2.5 Anacardium excelsum:

For *Anacardium excelsum*, there were no significant differences in regression slopes between treatments for the ln(dbh) function (F = 0.036, p =0.965), or for the ln(basal) function (F = 1.998, p =0.157). However, for the ln(height) function, treatments differed significantly (F = 7.619, p = 0.003). In this case, the monoculture regression was the steepest, followed by 3-sp and then 6-sp (Table 20, Fig.10). Differences were detected between 3-sp and 6-sp (p = 0.035) and between monoculture and 6-species (p = 0.003), but not between monoculture and 3 species (p = 0.760) (Table 21).

Table 20: Comparing regressions across treatments for ln(DW) = αln(H), for Ae

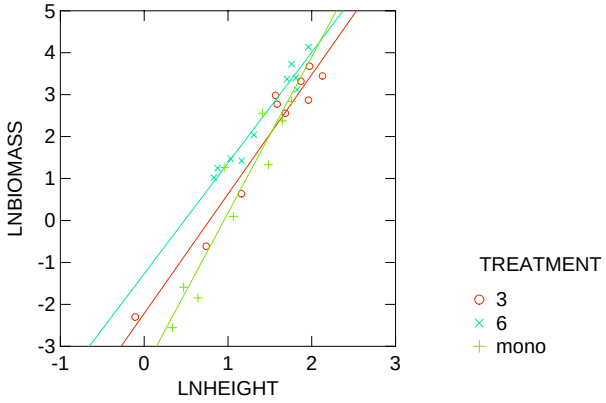
Treatment	Mono*	3-sp	6-sp
n	9	10	10
b	3.728	2.849	2.643
r^2 of regression	0.898	0.951	0.951

*1 outlier removed (AE 2-3 13-11)

Table 21: Matrix of pairwise comparison probabilities (Bonferroni Test)

	3-sp	6-sp	mono
3-sp	1.000		
6-sp	0.035	1.000	
mono	0.760	0.003	1.000

Fig. 10: ln(DW) = αln(H) plotted by treatment for Ae



DISCUSSION

4.1 Regression equations:

4.1.1 Specific Wood Density

Wood specific density has been used as a parameter in multi-species models to predict above ground biomass (Chave et *al*. 2005). In these models, species-level average wood densities were used. In species-specific models, however, this value is the same for all individuals, i.e. it is a constant rather than a variable. It was for this reason that it had no effect on r^2 values in our equations. It would be possible to use wood specific density in species-specific models if it were measured on each tree individually. However, this would be slightly destructive (unless done with a tree corer) and highly time-consuming. We therefore suggest that specific wood density be excluded from species-specific allometric equations.

4.1.2 Height

Authors hesitate to include height in allometric models developed for natural forests, as height is quite hard to measure in mature plots with trees of random ages and species. However, our best-fit models for predicting AGB for Ls, Tr, Hc and Ae were all developed using height. The fact that height increased r^2 values does not only imply that height has a strong correlation to biomass. The strong height-biomass association also means that the height measurements were accurate. It seems logical that height would be much easier to measure in young plantations than in mature natural forests. Trees being all evenly spaced and relatively short in plantations, it is much easier to identify the crown from a distance, allowing the use of simple tree height measuring instruments.

4.1.3 Sum of Diameters of all Trunks (DALL)

Diameter of all trunks was never used in our best fitting equations for predicting AGB. We also never came across DALL in the literature. Trees often have a high variability in architecture. It is often very confusing to distinguish from low branches with vertical orientation and secondary trunks. High error rates in measurements of this

parameter are therefore quite probable. DBH, being the diameter of the largest trunk of the tree seems to be much more constantly highly correlated to AGB in our data sets. In fact, as height, DBH was used in 4 out of 6 of our best-fit models for predicting AGB.

4.1.4 Basal Diameter

We considered basal diameter in this study because we thought that it might be a better predictor than DBH in a plantation where many trees are young and between 1 and 2 meters tall. DBH in most forestry studies is measured on mature trunks and therefore relatively low on the tree in comparison to total height. On a population of trees that vary in height from 1 m tall to 14 m tall (as is the case in Sardinilla), we thought that the location of the diameter measurement relative to the total height of the tree might be too variable to be a good biomass predictor. For this reason, we measured both DBH and basal diameter in order to compare their ability to predict biomass.

Basal diameter was only used in our model for Cm. This was the model for which we had the most outliers. Even after the removal of the 2 outliers that held unrealistic values and 2 other outliers, the value of r^2 was still the second lowest after Tr. This suggests that there is high variability between individuals of Cm in the relationship between basal diameter and AGB. The exclusion of outliers that were not unrealistic increased the value of r^2 but to a cost: the resulting model was based on a smaller and potentially non-random sample. This means that estimates of Cm biomass for the entire plantation may have a higher percentage of error than estimations conducted for other species with different models. We think that basal diameter may not have been such a strong parameter because of the influence of the root system on diameter at the ground level. Although the species studied in the Sardinilla project did not exhibit strong buttressing, such physiology would render basal diameter measurements quite unreliable for AGB predictions in many other species.

4.1.5 Variation Between Species-Specific Equations

The fact that no two species had the same best fitting allometric equation for predicting AGB justifies the importance of developing species-specific models. Different species allocate energy and resources to different parts of the plant depending upon each

tree's life strategy. General models do not take this in consideration and are therefore prone to hold more error than species-specific models. In the context of plantations where all species are known and easily identifiable, this argument is even more valid.

4.1.6 Extra Parameter Trade-off

It is important to make a cost-benefit analysis for every extra parameter included in a model. Gains in r^2 values may not be worth the while of the supplemental field time required for extra measurements. Plantations hold thousands of trees. In a scientific context, it is probably beneficial to have the absolute most precise model because these same models will help increase our understanding of the global carbon cycle. However, when models are to be used by farmers wanting to know how much their plantation plots are worth on the carbon credit market, field time must be used efficiently. That is why it is crucial to find very simple but efficient AGB predictive models.

4.1.7 Range of our Models

It is important to keep in mind that our regression models were developed from trees that were 5 years old. The objective was to create predictors of AGB for young plantations. It is not valid to extend linear regressions beyond the combined range of the x variables used to develop them (Zar 1999). Therefore our models should not be used for mature forests (natural or plantation) until they are tested in a similar manner as our experiment. Allometry is likely to change with age as the accessibility to nutrients, water and sun change due to the modifying effect of the growing trees on their environment. Furthermore, the physical constraints of increasing weight may cause trees allometry to shift with age.

4.2 Effects of biodiversity on allometry

For each species (excluding Ca), three simple regressions were fitted: ln(biomass) as a function of ln(height), ln(dbh), and ln(basal diameter) respectively. For each of these relationships, separate regressions were derived for each treatment (monoculture, 3-species, and 6-species) and analysis of covariance was used to determine whether their slopes differed significantly. Of the 15 regressions that we tested in this way, only 3

showed significant differences among treatments: ln(DW) = αln(height) for Ae, and Cm, and ln(DW) = αln(DBH) for Cm. One case (ln(DW) = αln(DBH) for Ls) was nearly significant (p=0.052). It is unclear at this point whether these results mean that allometry is relatively conserved regardless of biodiversity treatment, or whether we failed to find significant differences in a majority of cases simply because our sample sizes were too small. The fact that some species, for example Hc and Tr, showed no significant differences in allometry with treatment, whereas others, for example Cm, exhibited large changes, suggests that physiology may be a phenotypically plastic trait in some species, but not in others. In other words, some species may grow in different ways (resulting in altered allometric relationships) depending on the species and/or functional identity of their neighbours, while others may retain a rigid body plan (and thus invariant allometry) regardless of environmental variables such as species richness of neighbours.

In the three cases where we detected significant differences in allometry with changing biodiversity levels, the least diverse plots showed the steepest relationships between biomass and the tested predictor variables. For Ae, biomass increased significantly faster with height in monoculture plots than in 3-species or 6-species plots. This suggests that lateral growth (either through the thickening of the primary trunk or the growth of lateral branches) accompanying increases in height is more significant in monoculture rather than mixed-species plots for this species. For Cm, biomass increased most rapidly in function of both height and dbh in monoculture plots. In other words, a given increase in height or diameter in a monoculture plot will result in a greater increase in biomass than it would for equivalent growth in a higher diversity plot. This implies more allocation of weight to lateral branches in proportion to trunk widening and vertical growth in monocultures compared to high diversity plots. In contrast to Ae and Cm, Ls individuals showed the most rapid increases in biomass in relation to dbh in 6-species plots.

While these results do not convey any information regarding variations in absolute growth rates between treatments, they do show that patterns of growth may vary with biodiversity, for certain species at least. Ae and Cm seem to allocate more resources to lateral growth (increases in DBH, or growth of branches) in monocultures, and more resources to vertical growth (increases in total height) in mixed-species plots. This

difference could be important to foresters growing trees for timber, in which case it is desirable to maximize vertical growth.

At this point, there is insufficient data to draw conclusions concerning the causes and mechanisms behind the shifts in allometry that we observed with increasing biodiversity. However, we can speculate that, for Cm, Ae, and Ls individuals, the species and/or functional identity of neighbours may significantly affect the nature and intensity of inter-individual competition for water, light, and nutrient resources, resulting in altered growth plans. The changes that we detected (e.g. shift in resources allocation between vertical and lateral growth) may be the result of adaptations to competition. For example, a greater investment in vertical growth could be a mechanism to outcompete neighbours for light, while a reduction in lateral branching could be due to crowding and shading from neighbours. It is not clear whether Hc, and Tr do not alter their growth patterns in response to changing biodiversity because they are not as vulnerable to competition from other species, or simply because their physiology is not plastic enough to respond to these pressures.

CONCLUSIONS

Best-fitting equations for predicting biomass differed for every species studied in the Sardinilla Project; therefore, we recommend the use of species-specific models for estimating carbon stocks in the Sardinilla Carbon Project and in young tropical plantations in general. The non-destructive parameters that best predicted AGB were height and DBH, which were used in constructing four of the six of the models with the highest r^2 values. Our models should not be applied beyond the range of the variables that were used to construct them, i.e. they should not be used in mature forests without prior testing. Finally, in three cases, biodiversity had a significant effect on tree allometry. More research is needed to determine the extent of these differences and their potential causes. In general, more attention must be focussed on quantifying and modeling carbon stocks and fluxes in the tropics, as they represent a significant portion of global carbon reserves: one that is increasingly threatened by deforestation and other land use changes.

REFERENCES

Brown et al., S., Gillespie, A. and Lugo, A. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. Forest Science. 35(4): 881-902.

Chave, J. et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia. 145(1): 87-99.

Ehrlich, P.R. and Ehrlich, A. H. 1981. Extinction. The causes of consequences of the disappearance of species. Random House, New York. (Cited in Wardle et al. 1997)

Grace J. 2004. Understanding and managing the global carbon cycle. Journal of Ecology. 92: 189-202.

Grime, J. P. 1997. Biodiversity and ecosystem function: the debate deepens. Science 277: 1260-1261.

Harmon M. E. 2001. Carbon sequestration in forests. Journal of Forestry. 99(4): 24-29.

Hector, A. et al. 1999. Plant Diversity and Productivity Experiments in European Grasslands. Science 286: 1123-1126.

Kettreings, Q. M. et *al*. 2001. Reducing uncertainty in the use of allometric biomass equations for predicting aboveground tree biomass in mixed secondary forests. Forest Ecology and Management. 146: 199-209.

Kraenzel M. et *al.* 2003. Carbon storage of harvest-age teak (*Tectona grandis*) plantations, Panama. Forest Ecology and Management. 173: 213-225.

Lawton, J. H. 1994. What do species do in ecosystems? Oikos 71: 367-374
(Cited in Wardle et al. 1997)

Lawton, J. H. and Brown et al., V. K. 1993. Redundancy in ecosystems - In: Schulze, E. D. and Mooney, H. A. (eds), Biodiversity and ecosystem function. Springer-Verlag, Berlin, pp. 255-270.
(Cited in Wardle et al. 1997)

Loreau, M. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294: 804-808.

Loreau, M. and Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412: 72-75.

Nelson et al., B. W. et al. 1999. Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. Forest Ecology and Management 177: 149-167.

Overman, M.P.J. Witte, L.J.H. Saldarriaga, G.J. 1994. Evaluation of regression models for aboveground biomass determination in Amazon rainforest. Journal of Tropical Ecology. 10(2): 207-218.

Potvin, C. 2003. Sardinilla Carbon Project website.
http://www.biology.mcgill.ca/faculty/potvin/sardinilla.htm

Raich, J.W. and Nadelhoffer, K.J. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology. 70(5): 1346-1354.

Randerson J.T. et *al.* 2002. Net ecosystem production: a comprehensive measure of net carbon accumulation by ecosystems. Ecological Applications. 12(4): 937-947.

Schimel, D. et al. 1995. The Science of Climate Change (IPCC-1995 Vol. 1). Cambridge University Press, pp. 76-86. (Cited in Nelson et al. 1999)

Ter-Mikaelian, M.T. 1997. Biomass equations for 65 North American tree species. Forest Ecology and Management. 97: 1-24.

Wardle, D. A., Bonner, K. I., and Nicholson, K.S. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79: 247-258.

West, R. C. And J.P. Augelli. 1989. Middle America: Its Lands and Peoples. 3rd Ed. Prentice Hall: Englewood Cliffs, Pp. 457-468.

Wood Density Database. http://www.worldagroforestry.org/sea/Products/AFDbases/WD/

Zar, J. H. 1999. Biostatistical Analysis 4th ed. Prentice Hall. Upper Saddle River.

APPENDIX

Host Institution Co-ordinates:

Smithsonian Tropical Research Institute

Roosvelt Ave.
Tupper Building – 401
Balboa, Ancón
Panamá, República de Panamá
Phone: +507 212-8000
Fax: +507 212-8148
www.stri.org

Catherine Potvin

Department of Biology
Stewart Biology Building
1205 Dr Penfield Avenue
Room W4-7
Montreal, Quebec, H3A 1B1
Phone: (514) 398-3730
catherine.potvin@mcgill.ca

Chronology of Activities:

January 10:

- First visit to Sardinilla with Jose-Luis Bonilla
- Explored plantation and were introduced to plantation design and species

January 19-20:

- Research and planning at STRI (Background information)
- Visited Sardinilla with Catherine Potvin, discussed methodology

January 26-27:

- Research and planning at STRI (Methods)

February 1:

- Purchased field equipment

February 2-3:

- Meeting with Catherine Potvin to finalize methods

- Selection of trees to cut

February 4:

- Purchased field equipment

February 5-10:

- Harvested, measured and weighed all trees from monoculture and 3-species plots
- Collected, catalogued and weighed all fresh leaf and trunk samples

February 16-17:

- Finalized progress report
- Collected samples from Sardinilla for drying

February 23-24:

- Work on informal presentation

March 9-10:

- Informal presentations

March 16-17:

- Drying samples, weighing samples, data entry

March 20-24:

- Data collection in Sardinilla

March 30-31:

- Data collection for leaf specific area at BCI

April 13,14:

- Drying and weighing samples

April 17-23:

- Data analysis, preparation of final report

April 24:

- Internship symposium

Total Number of Days Spent on Project: 41

Number of Days Spent in the Field: 16

Thank-you notes:

Catherine Potvin

Department of Biology

Stewart Biology Building

1205 Dr Penfield Avenue

Room W4-7

Montreal, Quebec, H3A 1B1

Jose-Luis Bonilla

No Current permanent address; please deliver care of Catherine Potvin (above)

.

Executive summary
Benjamin Wadham Gagnon
& Diana Sharpe

Estimating carbon stocks in tropical hardwood plantations

Our internship for PFSS 2006 was with the Smithsonian Tropical Research Institute (STRI). More specifically, we worked with Dr. Catherine Potvin, a biology professor at McGill University. The STRI headquarters, as well as Dr Potvin's office are located in the Tupper research centre in Panama City.

There are growing concerns worldwide about the effects of greenhouse gases, especially carbon dioxide, on the stability of our climate. It is thought that forest ecosystems could be a sink capable of reducing levels of atmospheric carbon and forestalling climate change. In the tropics, the conversion of pasture to plantation is seen as a means to increase the area of forested land, thereby increasing carbon sequestration. To better evaluate the potential of plantations to sequester carbon, it is crucial that allometric models be developed that are capable of accurately estimating biomass.

Our project had two objectives. Firstly, we worked at developing species-specific allometric models that predict above-ground biomass (AGB) from non destructive and easily measurable parameters such as height, diameter at breast height (DBH), DBH of all trunks, and basal diameter. These models were developed for the six species found in the Sardinilla plantation. Our second objective was to determine whether biodiversity has an effect on allometric relations.

Our sampling was done within the Sardinilla Carbon Project plantation, located in the Buena Vista region of Panama. This plantation contains six species which are distributed throughout plots in combinations of 3, 6 and single species. Dry weights for 150 trees (10 trees per species, per treatment) were estimated by felling and weighing individuals on the field. Diameter and height were recorded at the same time as tree harvesting. Linear regression analysis was used to construct the best fitting species-specific models to predict biomass from field parameters. Then, to assess whether biodiversity had an effect on tree allometry, linear regressions were developed for each different biodiversity treatment (1, 3, and 6 species) and their slopes compared for significant difference by analysis of covariance.

The r^2 value of our allometric models varied from 0.995 to 0.837. Models varied significantly among species, both in terms of their precision, and the parameters they employed. Some parameters were more useful than others in predicting AGB: DBH of all trunks was never used as a parameter while height and DBH were used 4 times each. In 12 out of 15 cases, allometric regressions did not differ significantly among treatments. In the 3 cases where biodiversity had a significant effect on biometry, the steepest relationships between biomass and predictor variables were observed in monoculture plots.

For estimating carbon stocks in tropical plantations, we recommend the use of species-specific (versus multispecies) allometric models that include tree height and diameter as principal parameters. We also suggest that, for some species, plot biodiversity level be considered as a potential variable in future AGB models.

Estimaciones de reservas de carbono en plantaciones tropicales

Nuestra pasantilla del PFSS de 2006 fue con el Instituto Smithsonian de Investigaciones Tropicales. Más precisamente, trabajamos con Dr. Catherine Potvin, una profesora de biología de la Universidad de McGill. La sede administrativa de STRI, además de la oficina de la Dra. Potvin, están ubicados en el centro de investigaciones Tupper en la ciudad de Panamá.

Hay preocupaciones crecientes en todo el mundo sobre los efectos de gasas de invernadero, especialmente el dióxido de carbono, sobre la estabilidad del clima mundial. Se piensa que los ecosistemas forestales se podrían están hundiendo y que sea capaz de reducir niveles de carbono atmosférico y demorar el cambio climático. En las regiones tropicales, la transformación de potreros en plantaciones se ve como una manera de aumentar el área de tierra reforestada, y así aumentar la secuestración de carbono. Para poder evaluar mejor el potencial de plantaciones para secuestrar carbono, es necesario de desarrollar modelos biométricos que pueden predecir la biomasa con precisión.

Nuestro proyecto tuvo dos objetivos. Primero, tratamos de desarrollar modelos biométricos específicos al nivel de especie para predecir la biomasa arriba del suelo (BAS) desde parámetros no destructivos y fáciles a medir, como la altura, el diámetro a altura de pecho (DAP), DAP de todos los truncos, y diámetro basal. Estos modelos fueron desarrollados para las especies que están en la plantación en Sardinilla. Nuestro segundo objetivo fue de determinar si la biodiversidad tiene un efecto sobre relaciones biométricas.

Todas las muestras fueron tomadas en la plantación en Sardinilla, ubicada en la región Buena Vista de Panamá. Esta plantación contiene seis especies que están distribuidas por parcelas en combinaciones de seis, tres, y una especie. El peso seco para 150 árboles (10 árboles por tratamiento por especie) fue estimado al cortar y pesar dichos árboles en el campo. El diámetro y la altura se midieron al mismo tiempo en el campo. El análisis de regresión lineal fue usado para construir relaciones biométricas para predecir biomasa desde diámetro y altura. Entonces, para determinar si la biodiversidad tuvo un efecto sobre la biometría de los árboles, regresiones lineales fueron desarrolladas para cada diferente nivel de biodiversidad (1,3 y 6 especies) y comparadas por análisis de covarianza

El valor de r^2 de nuestros modelos biométricos varió de 0.995 a 0.837. Los modelos variaron significativamente entre las especies, en función de su precisión, y en función de los parámetros que usaron. Algunos parámetros fueron más útiles que otros para predecir la BAS: el DAP de todos los truncos nunca se usó, mientras que la altura y el DAP se usaron 4 veces cada uno. En 12 de 15 casos, las relaciones biométricas no fueron significativamente diferentes entre tratamientos. En los 3 casos donde la biodiversidad tenía un efecto significativo sobre la biometría, las relaciones más fuertes entre biomasa y las otras variables se observaron en las parcelas de monocultivo.

Para estimar reservas de carbono en plantaciones tropicales, recomendamos el uso de modelos biométricos específicos al nivel de especie (y no generales) que incluyen la altura y el diámetro como parámetros principales. Sugerimos también que, para algunas especies, la biodiversidad de cada parcela debe estar considerado como un variable potencial en futuros modelos de BAS.