Biogeosciences Discuss., 7, C5463–C5478, 2011
www.biogeosciences-discuss.net/7/C5463/2011/

Biogeosciences Discussions

Interactive comment on "Controls over aboveground forest carbon density on Barro Colorado Island, Panama" *by* J. Mascaro et al.

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Received and published: 4 May 2011

Dear Editors,

Below we respond in detail to each of the criticisms raised by the reviewers. While the MS was in review, we also made a number of other updates to our analyses that we detail here. We emphasize that these improvements have not led to any qualitative changes in our results:

1) We will correct a clerical error (128 + 29 = 157 not 158 plots, page 8824, line 1).

2) We will make a change in the methodological approach to curve fitting. We had previously used a linear fit on log-transformed MCH and ACD data. We will update to a nonlinear fitting approach that, like log-transformation, allows for non-arithmetic error

structure that we have found to be common in MCH and AGB data (i.e., not unlike tree allometry data, Chave et al. 2005). Both approaches are reasonable, but we find the new approach preferable because it tends to be more stable at high MCH (i.e., where most carbon is stored).

3) We have updated the field calibration data used for the model. We had previously used the 2005 census data for the 50ha plot, but the 2010 census data (closer to our LiDAR flight of 2009) became available during the review period. This change had no qualitative effect on the results of our multiple regression – although the overall carbon density measured for BCI did decline because of real mortality in the 50ha plot (i.e., the LiDAR saw low canopies in 2009 in places where large trees had been present in 2005, causing our original estimates to be inflated). This change improved the overall fit (r2 increased from 0.77 to 0.85, RMSE decreased from 29 to 17). We have attached the new model which will be a revised figure in our resubmission.

4) Given that nearly 10 years have lapsed since some height measurements were taken in the 50ha plot – we will no longer use these height measurements directly for individual trees. All tree heights will now be estimated with an allometric model based on synchronous diameter and height measurements.

Here we respond to each of the points raised by the reviewers (their comments in italics, our responses in underlined text).

Reviewer 1 (Scott Stark):

"Controls over . . . carbon density on [BCI]" presents an aerial lidar-derived regional estimate of aboveground carbon stocks and carbon density (ACD) as well as spatial structure in ACD. Furthermore, this paper addresses the question of controls over the spatial structure of ACD on Barro Colorado Island; factors addressed can be grouped into physiography and land-use history categories. In the physiography category maps of continuous slope estimates and categorical parent materials and soil type/textural variables are considered while land-use history - available through the long record of research at BCI - includes regions of old growth and relatively old second growth forest (two categories spanning 80 - 130yrs). Results show that both basic categories are important for the distribution of aboveground biomass on the island, with slope followed by forest age and soil categories predicting up to 30% of variability in ACD (at the largest scale of spatial aggregation considered).

The paper is well structured and clearly presented. The findings that slope, soil factors, and stand age are related to ACD over this spatial extent are novel and important and have not been possible before the development of lidar for this application.

Specific Comments:

In some tropical regions, e.g., the central Amazon, the height and seasonal dynamics of the local water table may be important to forest structure and function. In the extreme these soil hydrological factors may be associated with specialized riparian communities like igapo and varzea but they may also play a role in terra firme forests of different elevations and water table characteristics. While this study describes the drainage of soil types in table 2 there is relatively little discussion of potential hydrological factors. One factor that might capture something about soil hydrology on BCI is simply elevation above the lake; in the Amazon, for example, height above the nearest drainage (HAND, derived from radar, Renno et al 2008, doi:10.1016/j.rse.2008.03.018) has been correlated with the depth of the water table. Would this add predictability to the model or is there a good argument to leave out this factor? Perhaps in future studies mapping the distribution of deciduous trees and potentially lianas that might be expected to respond strongly to local hydrology–along with measurable hydrological factors–might help inform estimates of hydrological effects on ACD.

We agree that height above the lake may be an important factor. We excluded it here (and went further by masking all areas < 50 m from the shoreline) because we believed hydrology on BCI (due to the importance of Gatun Lake) was not likely to representative of a general relationship between carbon density and site factors. However, we will

clarify in the discussion that the slope effect found may partly be attributable to higher soil moisture retention on steeper slopes. Specifically, we will note that: “In addition to nutrient release, water availability appears to be higher on sloped terrain on BCI relative to the hilltop and plateau, particularly during the dry season. Hubbell and Foster (1983) found higher soil water potential on sloped terrain on BCI, as well as higher leaf water potentials. Daws et al. (2002) also found that sloped areas consistently had higher water availability than flat areas. They further found that sloped areas experienced less extreme seasonality than flat terrain because the increased water availability mitigated the effects of the dry season. All sampled sloped areas experienced < 50 drought days per year (defined as those with a soil water potential of less than -1500 kPa), while more than half of sampled plateau areas experienced > 50 drought days per year, and several experienced > 80 drought days.”

A potentially important citation for this paper is Castilho et al. 2006 “Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography.” This study analyzes a series of 1ha plots arrayed on a ‘mega-grid’ covering 10X10km of forest. Plots are stratiïňĄed by elevation–and follow elevation isocontours–in drainage associated ‘micro’ topography typical of the region. Castilho et al. find that 20% of variation in ACD is related to topography and soil but they do not find a slope effect. I am not sure where their slope plots fall in the spectrum considered by this study, some are certainly very steep but not all. I am also not sure if these slopes ‘expose’ bedrock to the same extent nor do I know if they are associated with the same nutrient dynamics as in BCI–the reference explicitly addresses the nutrient availabilities though.

We appreciate that the reviewer pointed us to this important study. De Castilho et al. did in fact find fewer emergent trees on steep slopes and we will treat this paper in our discussion as follows: “One Amazonian study found no effect of slope of total carbon stocks (de Castilho et al., 2006), although they found that emergent trees were less abundant - and smaller trees more abundant - on steeper terrain, suggesting that forests in sloped areas were more exposed to periodic mass wasting and canopy damage." In contrast, on BCI, large trees are more abundant on steeper slopes, which also have higher biomass. There is no obvious reasons why patterns differ between these sites, but it is possible that the soil structure and mass wasting in that part of the Amazon makes slope environments hostile to long-lived emergent trees.

The correlation of predictors presented in Table 5 does not seem to control for spatial structure as the rarefaction method used in the main analysis does. I do not believe, however, that the resolution of this question is central to the article nor the main conclusions of the article.

The reviewer is correct that the correlation of predictors does not control for spatial structure – instead, it presents exactly that correlation (including spatial structure) that is present in the full dataset analyzed. We believe this is the most informative way to provide information on these correlations.

Were any interaction terms considered in the main statistical analysis? My limited knowledge of linear modeling suggest that significant correlations can influence estimates of main effects, and it seems that some of these factors might interact. The general conclusion of the paper is likely insensitive to this potential analysis issue, though.

We explored versions of the model that incorporated interactions, but we excluded these in our final model because they (1) did not sufficiently alter the overall model significance, or the significance levels or relative magnitude of the main effects to warrant inclusion, and (2) were far more spatially auto correlated and therefore generally did not survive the rarefaction. Thus, we were confident (as suggested by the reviewer) that including these interactions increased the complexity of the model without influencing the main conclusions of the study, and therefore decided to omit them.

While Agua Salud is used, along with the BCI 50ha plot, as training data for the lidar biomass prediction, it seemed that the Agua Salud sites were not considered in the analysis of ACD controls. I wonder if such 'low end' biomass and height value sites

would be represented on BCI? What happens to the r2 and RMSE of the mean canopy height vs. biomass relationship if only the BCI plots are included?

We did note (page 8826, lines 22-24) that the RMSE of the BCI data alone is higher than the overall RMSE (now 19 v. 17) and the Agua Salud data alone is much lower (now 8 v. 17). We specifically included Agua Salud data in order to calibrate our model more effectively across the full range possible on BCI (i.e., but not found in the 50-ha plot or other monitoring plots on BCI). The functional composition of the Agua Salud area (e.g., mean wood density, somewhat to our surprise) is very similar to that in the 50-ha plot, so we believe that it is appropriate to link these datasets for calibration purposes.

Technical Corrections: Table 5 - model 'parameters' should be changed to model 'variables.'

Will be corrected.

'Imperfect' is used to describe the drainage of shallow mottled clay in table 2. I suggest choosing a different term unless this is technical.

Will be changed to "poorly drained".

On pg 8832 line 19 add of between 'some' and 'these'.

Will be corrected.

Reviewer 2 comments

"Controls over aboveground forest carbon density on Barro Colorado Island, Panama" By; Mascaro et al. General Comments: The paper discusses different controls on the aboveground biomass carbon density (ACD) in Barro Colorado Island. The biomass density is derived from airborne lidar measurements calibrated with height-biomass allometry developed from various plot data in the study area and mapped over the entire island at different spatial resolution. The controlling variables are slope angle, soil texture, bedrock, and forest age. The paper has the potential of providing interesting information about the landscape variations of biomass and approaches that can be implemented in other regions. However, the paper suffers from major methodological errors in analyzing the lidar data that may impact the magnitude of biomass distribution and probably change the entire results and findings of the paper.

Detail Comments:

1.There is a body of literature on the biotic and abiotic factors that impact forest structure, such as size-frequency distribution of trees, and spatial organization of structure, gap size and dynamics, and wood density, all variables that define forest biomass variations. It is important that the authors refer to these literature and highlight their findings as some are relevant and others may be different and in contradiction to what they have found in their analysis. I will point these out later.

We strongly agree with the reviewer, and we do (and will) point to several studies on the biotic and abiotic drivers of tropical forest biomass/carbon stocks, including in the introduction as we establish the motivation for this study (page 8819, lines 6-10), specifically citing Laurance (line 10, as the reviewer points to below), and specifically citing Clark and Clark (page 8820, line 7). We also emphasize that our results stress that abiotic factors deserve a second look in the tropical literature (page 8834, lines 1-12). We will add treatment of de Castilho et al. (2006) in the introduction and discussion in response to notes from both reviewers.

It is true that most of these results (e.g. Clark & Clark, 2000 ; Castilho et al., 2006; Chave et al., 2001; Laurance et al., 1999; Stagen et al., 2009; etc.) are based on plot data. However, it is not clear why plots well-designed across the soil, elevation, slope, or other factors may not be the best way to address this problem. I will try to explain this in other points.

We agree that plot arrays that are sufficiently well-designed and sufficiently large could in principle address these questions. However, such plot data are rare, if they exist at

all. As the reviewer points out – “plots well-designed across the soil, elevation, slope or other factors” would indeed be needed, and most available plot networks were not designed with this intent. Further, the higher cost of ground-based inventory plots means that they simply do not exist on the scale of the LIDAR datasets we analyze here. And this scale is critical – our use of LiDAR data for a large area (>1200 ha) considerably increases statistical power and thus reduces type 2 error relative to field plot studies which invariably have lower total area and fewer points. For example, de Castilho et al. 2006 (to which the reviewer refers) found no slope effects on aboveground biomass when using 42 plots – but there is a significant relationship in their data if just one outlier is removed (OLS regression biomass v. slope after removing LO2T0). So is there in reality a slope effect in the landscape studied by de Castilho, or not? We would argue that the 42 plots in that study are insufficient to satisfactorily address this question.

2. The authors show how biomass varies over the landscape and how the variations can be explained by several variables. However, there is hardly any ecological, geological, and historical reasons are tested or discussed for these variations. For example, the authors mention that the reason biomass is larger on steeper slopes is because erosion rates may exceed weathering rates. However, they do not produce any evidence or show any data to support this. Therefore, it could not be used a sentence in the abstract. One can suggest this as a potential hypothesis in the discussion.

We will remove our hypothesis regarding erosion versus weathering rates from the abstract. We discuss this possibility in the discussion, along with two alternatives to give a more balanced view. Specifically, we will note that nutrient availability, water availability, and competition for light are all non-mutually exclusive factors that may explain our results, and discuss all three at length.

3. Mapping forest Biomass from Lidar data has several methodological problems that need to be addressed. It appears that the authors treated this part of the problem casually. However, this is an important part of the paper as they claim that the Lidar captures the biomass and its variations better than well-designed plots. Here are some

of my main concerns:

a. Height metrics calculated at 5 m resolution is meaningless when calculating forest biomass. The auto-correlation length of forest structure variations in BCI or similar forests is between 10-20 m about the average size of crowns. Waveforms or height metrics are meaningful if they are calculated beyond the scale of canopy gap dynamics, such as 0.25. It is important to analyze the height metrics and biomass at a scale where the structure is stable. In this study, the calibration plots are much larger than 5 m to start with, so I do not understand why the authors calculated the waveforms at 5 x 5 m resolutions.

There seems to have been some misunderstanding of our analyses, no doubt resulting from our inclusion of a figure that showed 5-m resolution carbon density. In fact, we ran no biomass/carbon analyses using 5m data - the minimum resolution analyzed is 30m (i.e., our calibration equation was applied to MCH data at 30m resolution and greater), well outside the range of tree crown diameters. We will re-organized section 2.3 so that this information is more prominently presented. Mean ACD island wide is quite stable when applying the equation at these resolutions (i.e., 95 Mg/ha at both 30m and 100m). To avoid confusion, we will replace our 5m-resolution carbon density figure with a 5m-resolution figure of canopy height – combined with 5m-resolution views of 12-17 and 2-7 m canopy density, these three figures (which will be combined into figure 2) will be intended to allow the reader to understand forest structure on BCI at high spatial resolution.

b. As mentioned above, biomass estimation are better at a scale where both the biomass and the allometries are stable. This scale varies in forests but they are greater than 50 m resolution (0.25 ha), much larger than the average crown size or the scale of canopy gap dynamics. The analysis performed by Chave et al., have shown the scale where biomass is beyond the scale of gap dynamics and stable in BCI. At small scales (5-20 m) the forest structure and biomass are extremely dynamic and can vary a lot from year to year because of the natural disturbance and changes within the canopy.

So, the ground data at 50 ha plot in 2005 will be very different than the lidar data in 2009 at the scale of less than 0.25 ha (if not, definitely different at 20 m or 5 m, resolutions). For biomass mapping, I recommend to redo the analysis for at least 0.25 ha.

Again, we ran no analyses on 5m-carbon/biomass data. We explored several resolutions of analysis, from 30m to 100m (page 8826, lines 5-16), and thus readers can easily explore the patterns pointed to by the reviewer. Additionally, the 2010 census data (only 1 year removed from our LiDAR flight in 2009), became available during the review period for this manuscript and thus we will update our calibration equation to reflect the ground data more closely related to our LiDAR flight.

c. The height metric used in this study is not as convincing as one expect. The authors have a powerful waveform data and they only used one metric that actually may be not the best to predict the biomass. Recent results from Lefsky et al. 2010 and others have shown a combination of metrics will provide higher accuracy in estimating biomass. MCH is also very sensitive to changes of forest structure at high resolution. In fact, RH100 can be more stable through time than MCH (as smaller, below canopy trees, affecting the overall forest structure, are more dynamic in the forest than then tall emergents).

We will clarify that we have found that MCH is slightly better than RH100 (i.e., height) at predicting carbon density, and thus we have used MCH (see also Asner et al. 2010b, 2011). For BCI, RH100 was correlated at a r2 of 0.84 versus 0.85 for MCH.

Figure 2 also confirms that the variations of the height metric at the BCI plots are much larger.

We point this out on page 8826, lines 22-24, however it is clear that a single model explains both datasets very well (revised overall RMSE with the 2010 data is $\sim$17 Mg/ha).

Without the Agua Salud data, the plot would be different, suggesting that one metric alone will large errors in estimating the biomass in BCI.

We state that prediction errors in the 50ha plot alone are RMSE = 29 Mg/ha (page 8826, lines 19-24). Since the 50ha plot actually has higher ACD than most of BCI, the errors across the island will be < 18 Mg/ha with our revised model based on 2010 field data.

d. The authors completely ignore the scale of analysis. They use biomass estimated at various size plots and calibrate the lidar data at 5 m resolution.

To the contrary, we paid great attention to the scale of the analyses, which the reviewer seems to have misunderstood. We did no calibration at 5 m. As we stated, we used the mean MCH in a given plot (either 0.1 (Agua Salud) or 0.36 ha (BCI) resolution) to calibrate the LiDAR data (page 8823, line 18 – page 8824, line 5). Further, our study considered patterns in LiDAR data at several spatial resolutions.

Again, Chave's paper and also other ecological papers including some from the co-author Muller-Landau will show that allometries are scale dependent unless applied at a scale biomass and structure are stable. As this is not an individual tree allometry, relationships developed at one plot size on the ground between height and biomass cannot be applied at the different resolution lidar data. I can understand combining different plot sizes to reduce the heteroscedasticity, but the algorithm developed cannot be applied reliably at the 5 m data.

Again, we did not use 5-m data in our analyses, and we will remove the 5-m resolution carbon figure, which was previously included for illustration. In our revised version, we will make clear that we applied the calibration equation only at 30m resolution and greater. It was at these resolutions that all analyses were run, and at these resolutions ACD is quite stable (new mean based on 2010 data is ∼95 Mg/ha across resolutions). It's difficult for us to understand exactly what the author is referring to in the absence of specific citations and clarification of what allometries are meant. It appears that by

"allometry" the reviewer means MCH-biomass relationships. These are not addressed by any previous paper by Chave or Muller-Landau. Previous work by Chave et al. 2001 and Chave et al. 2003 clearly shows the high spatial variability in aboveground biomass as estimated from plot data - but this in no way implies that MCH-biomass relationships would be spatially variable. Because of high spatial variability in biomass, both these papers advocate sampling large areas in order to better capture the true pattern of average biomass; we're confident Jerome Chave would be delighted to see data for > 1200 ha used to better characterize biomass for a site. The reference to work by co-author Muller-Landau perhaps is referring to Chave et al. 2008, on which she is a coauthor; this work too shows high spatial variation in biomass within and among plots, and uses bootstrapping over 0.25-ha subplots to develop appropriate confidence intervals. This is consistent with our approach calibrating the model at 0.36-ha resolution for mature forest plots.

It would be great to test what would happen if lidar data was aggregated to different resolutions (5 m, 10 m, 20m, 50 m) and the same calibration equations were applied. I am sure, you will definitely find difference in the final results.

We will clarify that we did precisely this - for resolutions of 30m and greater. Across these resolutions, mean ACD island wide is quite stable (∼95 Mg/ha across resolutions).

e. How about slopes? Have you considered using plots at different slopes to calibrate the lidar data? Will there be the same calibration between height metric and biomass regardless of slope? How do you know that you are not creating a bias in your relationship when you use a calibration equation from flat area (e.g. 50ha plot is located on a flat area relative to the rest of the island). Let's imagine, tree diameters are smaller on higher slope but the tree heights are not. This means that you may be over-estimating the biomass on higher slopes.

We agree that if allometric relationships between tree height and diameter were different on steep slopes versus flat areas, a bias may be introduced. We will add this point in the discussion. We will also note that a comparison of the diameter-to-height relationship between trees found in the 50ha plot (predominantly on flat terrain), and those found near the ARTS towers (at more exposed elevations) found no fundamental difference.

f. Finally, you use the lidar height data and map the biomass. It appears that both your ground and lidar map are not area corrected. In general, after calibrating your lidar data to biomass, you need to correct for the area over slopes. Otherwise, the biomass values are higher over steeper slopes. The biomass results are impacted by not including the area correction. In BCI, you can easily over-estimate the area of a 1-ha plot by 1-20% depending on the slope and if not corrected, you will end up comparing biomass over a larger area (on the slopes) with smaller area (flat surface). I suggest, the authors look at this problem carefully. In mapping biomass density, area correction is important.

In general, we will make several changes to clarify to the reader how the analyses were conducted, including in the methods and discussion. We agree that surface-area-adjusted biomass values, that is, biomass per surface area of ground, will always be lower on steeper slopes. However, this is not the way that biomass stocks (e.g., for carbon accounting) are typically reported in the literature: values of carbon storage (in Mg/ha) typically refer to stocks over a horizontal area, regardless of slope - including for previously published analyses of BCI carbon stocks and several references pointed to by the reviewer (see, e.g., Condit 1998, Clark and Clark 2000, Chave et al. 2003, de Castilho et al. 2006). This is particularly true in long-term forest inventory plots such as those in the CTFS network, most of which are gridded with survey equipment - as opposed other forestry projects where this issue is often ignored, thus giving surface-area-adjusted results by default (i.e., because plots are measured by line of sight along the ground). Of course, simply because these results are produced by default does not make them the only way to analyze stocks. Indeed, RAINFOR biomass data are mostly

in units of surface area, and this was noted by Malhi et al. (2006) as a key shortcoming of their maps of biomass density over horizontal area. However, to explore this issue further, we will add a supplementary analysis on “surface-area-adjusted carbon density.” After running this analysis, we have found that surface-area-adjusted carbon density is still significantly higher on steeper slopes on BCI (though obviously less than over horizontal area).

g. The analysis of 2-7 m and 12-17 m layers of the height profile is confusing. It is not clear where these numbers come from. What is the statistical significance of the selected height ranges when looking at the forest structure at different scales? What happens if you use slightly two different ranges? I recommend choosing height metrics such as percentiles of energy to compare forest structure over the landscape instead of fixed height ranges.

The purpose of this analysis is to give the reader a better understanding of the structural variation in forests over BCI. Using percentiles would, in our opinion, make the basic interpretation of such an analysis more difficult - rather than more clear. For example, our low vegetation density figure highlights areas with abundant vegetation close to the ground (our intent), but if percentiles were used, the figure could easily highlight gaps in the same manner as tall forests. We will clarify our terminology on this point by noting that although we refer hereafter to “mid-canopy” and “low-canopy”, these terms are relative to all island-wide vegetation (with a mean top-of-canopy height of $\sim$22 m) rather than local context.

4. I think most of the results may be impacted by the problems with the methodology described above. I am afraid; it is very difficult to evaluate the paper and its importance without correcting the errors associated with the data analysis. Since slope angle is the most significant predictor of biomass variation on the island as mentioned by the authors, I think most of the results presented under forest age, soil texture and bedrock are also impacted by problems of mapping biomass from lidar.

We will add an additional analysis (provided in a supplementary table) showing that slope remains significant as a controlling factor even after adjusting biomass for surface area. We will note specifically that “At 100-m resolution, the model collectively explained 27% of surface-area-adjusted ACD (versus 33% for normal ACD; F1,1038 = 42.0, P < 0.0001); the importance of slope in explaining ACD declined from 19% to 11% when considering surface-area-adjusted ACD.” However, we disagree with the premise of the reviewer that biomass variation in space can only be analyzed in a surface-area-adjusted sense. As we noted above, analyzing biomass over horizontal area is the approach taking for long-term monitoring plots (e.g., the 50-ha plot), and will carry legal standing in this way in a future carbon market (IPCC 2006).

5. The authors mention that the reason biomass is larger on steeper slopes is because erosion rates may exceed weathering rates. However, they do not produce any evidence or show any data to support this. Therefore, it could not be used as a sentence in the abstract. One can suggest this as a potential hypothesis in the discussion. I assume, if the analysis changes according to the suggestions and then biomass variation turn out to less dependent on the slope, the hypothesis will not be true.

We will modify our suggestion on erosion and weathering rates to make it clear we are proposing one hypothesis to explain our results (this was our original intent), and we will remove this suggestion from the abstract. We will also include additional hypotheses in the discussion. We will describe in the discussion that biomass remains significantly higher after adjusting for surface area.

Interactive comment on Biogeosciences Discuss., 7, 8817, 2010.

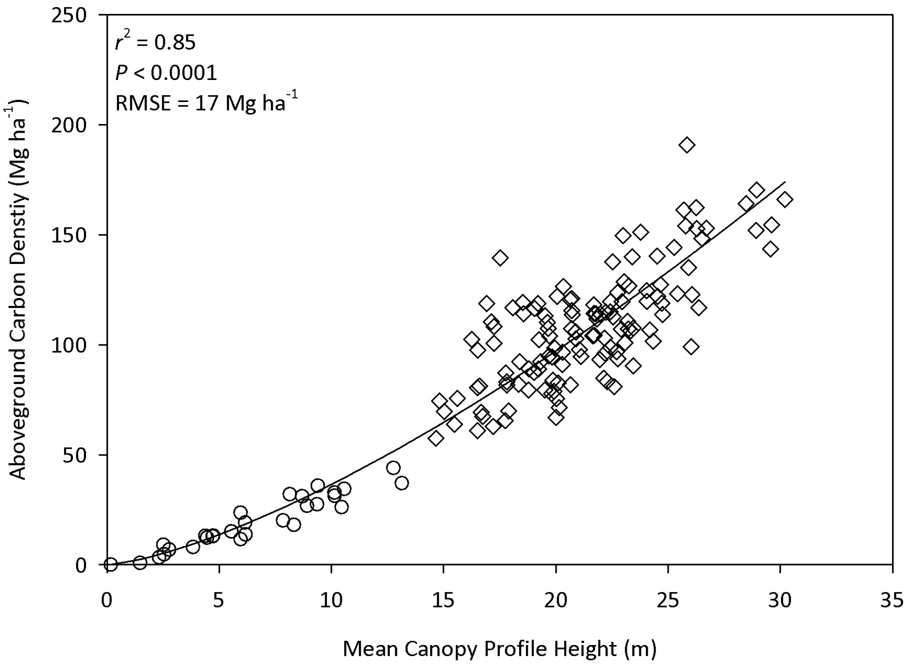

Fig. 1. new MCH-ACD model based on 2010 data