

Spatial and temporal variation in above-ground biomass in tropical forests in French Guiana

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Summary

Introduction

Reducing carbon emissions from deforestation in tropical forests is of central importance in efforts to combat climate change. Mechanisms such as REDD (Reducing Emissions from Deforestation and Forest Degradation) have been proposed to curb these carbon emissions from deforestation by financially compensating forest owners. However, key scientific challenges still need to be addressed in order to effectively implement REDD. In particular, one of the first challenges is to accurately estimate and monitor above-ground biomass (AGB) and associated carbon stocks in tropical forests. The main aims of this research were to study in French Guiana:

- 1) the effects of selective logging activity on forest AGB
- 2) the spatial variation in AGB of primary forests

Therefore, this study seeks to provide further knowledge about potential variation in AGB across tropical forests in French Guiana, which is crucial for future conservation of forest carbon stocks under REDD in the area.

Methods

For this research, field work was carried out in primary and secondary Terra Firme forest sites in the Trésor Nature Reserve and ONF forest area in the Kaw Mountains, North-Eastern French Guiana. A total of 9 Gentry plots were established in the Kaw Mountains. From the field data collected, the allometric equation of Chave et al. (2005) was used to calculate AGB. Moreover, AGB data from other forests sites in French Guiana were included into the analysis in order to address the main aims of this study: Turtle Mountain, Laussat, Nouragues, Regina and Trinité.

Results & Conclusion

In the Kaw Mountains, the mean AGB of trees ≥ 10 cm DBH in the secondary forest site (360.18 Mg/ha) was lower than in the primary forest sites in the Trésor Reserve (424.41 Mg/ha) and ONF area (414.46 Mg/ha). However, this difference in AGB was found to be non-significant. Nonetheless, a significant difference in forest structure was found due to the high density of very small trees ($\text{DBH} \leq 5\text{cm}$) in the secondary forest compared to both primary forests.

Furthermore, the AGB values in the secondary forests in the Turtle Mountain and Kaw Mountains were comparable, suggesting that recent selective logging in both forest sites caused similar amount of damage on forest AGB. More specifically, selective logging in the Turtle Mountain resulted in AGB losses from felled trees and collateral damage of about 87.11 Mg/ha two years after logging, representing 19% of the estimated 454.42 Mg/ha prior to logging. The mean rate of AGB accumulation 2-5 years post-logging was 0.22 Mg/ha/yr in the Turtle Mountain, which is extremely low in comparison to other studies. When applying the rate of AGB accumulation defined by Mazzei et al. (2010), the mean AGB in the logged forest in the Turtle Mountain was expected to recover to its initial value in about 35 years. Despite the lack of data prior to logging in the Kaw Mountains, more than 20 years would be required for the mean AGB in its secondary forest to recover to a similar value contained in its primary forest in 2011, which could be regarded as a reference. However, several limitations should be taken into consideration when interpreting these predictions in AGB recovery. In consequence, further research is needed to improve these predictions.

No significant difference was found between the mean AGB in the two primary forest sites (Trésor Reserve and ONF forest area) based on their spatial location in the Kaw Mountains. Consequently, the AGB values from these two primary forest sites were combined in order to compare the mean AGB in the Kaw Mountains with four other Terra Firme primary forest sites (Laussat, Nouragues, Regina and Trinité) across a larger spatial-scale in French Guiana.

However, no evidence of regional spatial patterns in AGB was detected among these geographically different forest sites. Furthermore, this study underlined a strong relationship between AGB and stand variables describing forest structure in Terra Firme forests across French Guiana. To conclude, future studies need to be carried out among major environmental gradients in order to examine the relative contribution of different environmental factors to potential spatial patterns in AGB across the Amazonian forest.

Acronyms

AGB	Aboveground biomass
DBH	Diameter at breast height
CO₂	Carbon dioxide
Mg	Megagram (tonne - 10 ⁶ grams)
Mt	Megatonne (million tonnes – 10 ¹² grams)
Pg	Petagram (billion tonnes - 10 ¹⁵ grams)
BAU	Business as usual
SE	Standard error of the mean
REDD+	Reducing emissions from deforestation and forest degradation in developing countries (including conservation, sustainable management of forests and enhancement of forest carbon stocks)
IPCC	Intergovernmental Panel on Climate Change
CIRAD	Centre de Coopération Internationale en Recherche Agronomique pour le Développement (French Agricultural Research Centre for International Development)
EcoFoG	Ecologie des Forêts de Guyane (Research Centre on the Ecology of the Forests of French Guiana)
ONF	Office National des Forêts (French State Forestry Service)

Preface

This research project was carried out within the context of my Master thesis in Sustainable Development with a specialization in Land Use, Environment and Biodiversity at Utrecht University, the Netherlands. Throughout the preparation and field research for this project, I worked with Alexandra Mitsiou, a fellow Master student at Utrecht University in Environmental Biology with a specialization in Ecology and Natural Resources Management. This research project was the second step of the pioneer project initiated the previous year by two Master students from Utrecht University, Anna Duden and Ineke Roeling. The general objective of both projects is to provide a basis for further research on the potential implementation of REDD (Reducing Emissions from Deforestation and Forest Degradation) in French Guiana.

This research project was supported by the Trésor Foundation, in order to investigate the carbon stocks in the Trésor Nature Reserve situated in the Kaw Mountains in French Guiana. We carried out field work in both the Trésor Nature Reserve and ONF forest area in the Kaw Mountains between February and May 2011. Upon our arrival in February with Vijko Lukkien, thesis supervisor and Project Manager of the Trésor Foundation, an MoU was signed with all the different organizations involved in this project in order to make official this multi-cooperation agreement: National Forestry Office (ONF), French Agricultural Research Centre for International Development (CIRAD), Research Centre on the Ecology of the Forests in French Guiana (EcoFoG) and World Wildlife Fund (WWF) French Guiana.

1. Introduction

1.1. *Climate change and tropical forests*

Climate change is one of the most pressing environmental concerns of the 21st century. There is a general scientific consensus that the increasing emissions of greenhouse gases (carbon dioxide, methane and nitrous oxide) due to human activities over the last decades are the main driver to this phenomenon (Lasco & Cardinosa, 2007; IPCC, 2007). More specifically, carbon dioxide is the most important anthropogenic greenhouse gas (IPCC, 2007).

Tropical forests cover a relatively small amount of the Earth's land surface (approximately 3.3%), of which 40% lies in the Amazon region (Kricher, 2011; Buchmann et al., 1997; Verweij et al., 2009). They are considered as one of the most important terrestrial carbon sinks. To illustrate this, it has been estimated that the Amazonian forest stores approximately 86 ± 17 petagrams of carbon (PgC) in biomass (Saatchi et al., 2007) with in addition 41-47 PgC stored in its soil organic matter (Salimon et al., 2011). However deforestation and forest degradation in the tropics are occurring at an alarming rate and are often driven by agricultural expansion and exploitation of forest resources (IPCC, 2007). It has been estimated that deforestation is removing annually about 0.6% of total forest area in the tropics, adding up to an estimated cumulative loss of 8.3% of tropical forests from 1990 to 2005 (FAO 2006; Butler, 2007; Myers, 2007). As a result, tropical deforestation and forest degradation represent the second largest source of global greenhouse gas emissions, contributing to 12-20% of anthropogenic carbon emissions (Houghton, 2005a; Ghazoul et al., 2010). More precisely, throughout the 1990s, tropical deforestation was estimated to have released about 1.4 Pg of carbon per year into the atmosphere (Gullison et al., 2007). Without the implementation of effective policies to lower current deforestation rates, future predictions about carbon emissions suggest that an additional 87 to 130 PgC is likely to be released into the atmosphere between 2000 and 2100 (Houghton, 2005b; Gullison et al., 2007). Thus, there is a rising concern to include measures which aim to reduce deforestation of tropical forests in future policies towards combating climate change (Griffiths, 2008). Furthermore, it is widely recognized that deforestation and forest degradation not only have a negative impact on carbon stocks but also on other essential environmental services such as biodiversity, hydrological cycles, erosion prevention or soil conservation (Salimon et al., 2011). All these detrimental ecological consequences underline the need to strengthen our efforts made towards the conservation of tropical forests.

The first step required to be able to implement measures aimed at reducing carbon emissions from deforestation is to accurately estimate and monitor the carbon stocks retained in tropical forests (Salimon et al., 2011). However, this first step of quantifying carbon stocks appears to be an important technical challenge. Different methods have been developed to measure and monitor forest carbon stocks but there is no scientific consensus about which one is most accurate (Gibbs et al., 2007). In consequence, there is a need to gain more knowledge on methods to accurately estimate carbon stocks as well as factors which may affect carbon stocks. Moreover, little is known yet about the effect of human activities on carbon stock levels. Therefore, this research in French Guiana aims to provide further knowledge and understanding of spatial and temporal variation in carbon stocks in tropical forests.

1.2. *Reducing Emissions from Deforestation and Forest Degradation (REDD)*

The adoption of the Kyoto Protocol in 1997 by a majority of the world's leader is generally considered as an important first step in combating human-induced climate change. This international agreement is linked to the United Nations Framework Convention on Climate Change (UNFCCC). The Kyoto protocol established binding targets for a reduction in global greenhouse gas emissions and entered into force in 2005 (Houghton, 2005b). However, reducing

emissions by preventing deforestation was excluded from the protocol primarily due to political and technical reasons (Ghazoul et al., 2010).

At the 11th Conference of the Parties (COP) of the UNFCCC in 2005, the Coalition for Rainforest Nations led by Papua New Guinea and Costa Rica presented a proposal aimed at reducing emissions from deforestation in developing countries (Cuypers et al., 2011). This proposal initiated international discussions over the inclusion of a framework for Reducing Emissions from Deforestation and Forest Degradation (REDD) in future climate policies. The concept of REDD is to provide financial incentives to help developing countries to conserve their forests rather than exploit them in a non-sustainable way (Ghazoul et al., 2010). More specifically, these financial incentives will promote developing countries to reduce national deforestation rates and associated carbon emissions relative to a national baseline. This national baseline defines the expected carbon emissions from deforestation and forest degradation if no efforts are carried out towards emission reductions, in other words under a business-as-usual scenario (Griscom et al., 2009). Consequently, countries that succeed in reducing their emissions below a fixed level (set by the crediting baseline) will be able to sell these carbon credits generated from emissions savings on the international carbon market. Figure 1 illustrates in more detail the role of the different REDD baselines.

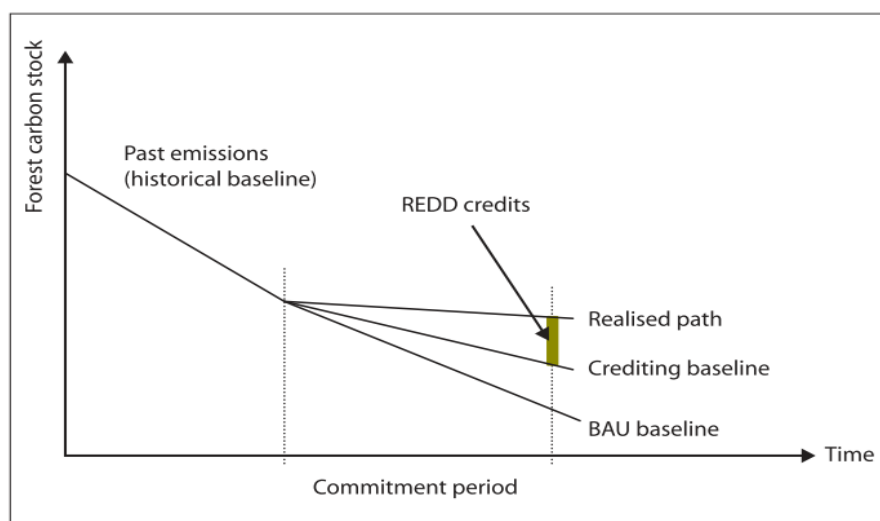


Figure 1. The different REDD baselines are represented in this figure. The historical baseline is the CO₂ emissions due to deforestation and degradation in the past years. This historical baseline is used to predict the business-as-usual (BAU) baseline under the absence of any efforts towards reducing emissions. The realised path represents the predicted CO₂ emissions following the implementation of REDD schemes to avoid deforestation. The difference between the BAU and the realised path shows the amount of carbon stock that remains intact in the forest due to the efforts of the REDD measures. The crediting baseline is set by the different parties involved and if emissions reductions attained are higher than this baseline, the countries will be rewarded with carbon credits (illustrated in green). Source: Angelsen (2008).

According to the US Ecosystem Market Place organization, the average price in 2010 of carbon credits transacted on the voluntary carbon market was 6 US\$ per tonne of CO₂ (Peters-Stanley et al., 2011). As a result, the substantial economic benefits from preserving tropical forests under REDD projects could have the potential to shift the balance of current economic market forces that favor deforestation activities over conservation (Malhi et al., 2008). Not only could REDD be a powerful instrument for climate mitigation by reducing carbon emissions from deforestation but also by contributing to additional climate-regulating services (i.e. precipitation, cloud formation, cooling through evapotranspiration). Moreover, by promoting forest conservation, REDD is likely to favor other ecosystem services such as biodiversity conservation, regulation of hydrological cycles or prevention of soil erosion (Malhi et al., 2008).

During the 2009 UNFCCC climate summit in Copenhagen, REDD was a major topic of discussion. Although no significant agreement over the potential implementation of REDD came about, overall there is a growing support for REDD and especially towards the extended REDD+ mechanism (Phelps et al., 2010). REDD+ was created in order to provide finance towards forest conservation as well as sustainable forest management and the enhancement of forest carbon stocks in existing forests (restoration). Through this mechanism, countries with low deforestation rates but high forest cover can be candidates for REDD+ projects.

The agreements achieved at the 2010 UNFCCC Cancun summit have defined REDD+ as a mechanism which *“encourages developing country Parties to contribute to mitigation actions in the forest sector by undertaking the following activities, as deemed appropriate by each Party and in accordance with their respective capabilities and national circumstances:*

- *Reducing emissions from deforestation;*
- *Reducing emissions from forest degradation;*
- *Conservation of forest carbon stocks;*
- *Sustainable management of forests;*
- *Enhancement of forest carbon stocks.”*

However these agreements remain modest due to the lack of any binding emission reduction targets for developed countries towards the implementation of REDD+ (Ghazoul et al., 2010). Furthermore, no agreements have been made over how REDD+ will be funded. Therefore all the different types of finance options remain open for discussion: market based approach, private finance, funds or a combination of either (Cuyper et al., 2011). Decisions over the potential financing of REDD+ through carbon markets have been postponed to the following climate summit. As a result, all current activities are carried out on a voluntary market basis. The global voluntary carbon market has been flourishing, with a total volume of 131.2Mt CO₂ emissions which was transacted over 2010. Suppliers reported that these volumes are 34% greater than in 2009 (Peters-Stanley et al., 2011). Furthermore, pioneer projects for REDD+ have been established in several countries with the objective to generate carbon credits for sale on the voluntary market (Phelps et al., 2010).

Although REDD+ is already rapidly evolving and has the potential to change tropical forest management on a global scale, it faces several challenges that should not be underestimated. Various issues related to technical, social, economic, ethical and governance aspects need to be further discussed in order to implement an effective REDD+ mechanism (Ghazoul et al., 2010). A list of the key challenges associated with REDD is summarized in Table 1, page 13 (Ghazoul et al., 2010).

As mentioned earlier, one of the first steps required towards the implementation of measures such as REDD+ is to accurately estimate and monitor the carbon stocks retained in tropical forests, in order to compare it with the carbon stocks related to alternative land uses. Carbon stock data per land use category are used to quantify the volume of avoided emissions and thus to assign appropriately carbon credits for avoided deforestation (Salimon et al., 2011). This represents an important technical challenge and several studies are attempting to accurately quantify carbon stocks in tropical forests. In particular, this study is relevant for providing knowledge on conservation and enhancement of forest carbon stocks within REDD+.

Table 1. Key challenges facing the effective implementation of REDD. Source: Ghazoul et al. (2010).

REDD challenge	Description
Ethical dilemma	REDD allows rich nations or corporations to 'absolve their sins' of carbon emissions through carbon offsetting with REDD credits. Some opponents of REDD argue that this would create disincentives for genuine efforts to reduce emissions or develop cleaner technologies.
Additionality	A key criterion for valuing carbon stocks for a REDD project is 'additionality' – the net emissions savings calculated using a baseline deforestation and carbon emission rates. Establishing the baseline deforestation rate is technically challenging. It might also be prone to political meddling that can inadvertently lead to environmentally damaging land-use policies ³³ . Furthermore, the criterion of additionality may also castigate countries that have maintained their forests prior to the establishment of baseline dates. Not only have they paid the opportunity cost of not using their lands, but they may have fewer opportunities to access REDD payments.
System leakages	The avoidance of deforestation in one area can displace it to another area. Such 'leakages' can be difficult to quantify. Unless there is coordination among REDD and other conservation strategies, forest clearing and degradation activities can still occur in areas not under REDD protection.
Permanence	It may be difficult to ensure the permanence of carbon storage after the REDD project period has ended or even within the project period. Forests and carbon stocks could be lost or degraded through human activities and also from natural events such as drought causing tree die-offs, or natural fires burning huge tracts of forests.
National sovereignty and native land rights	Participation in REDD schemes imposes long-term constraints on land use that can be construed as an infringement of a nation's sovereign right to manage the land according to its needs. To allay fears of compromising future development options and national sovereignty, some have suggested a carbon rental option as a temporary measure, whereby developed nations rent carbon credits from developing countries. Similarly, there is concern about the future rights of indigenous communities to access or use resources from forests protected under REDD, for traditional subsistence needs or other livelihood purposes, although the latest draft text of REDD offers better prospects in protecting the rights of indigenous peoples.
Equity	REDD rhetoric emphasizes the equitable distribution of REDD benefits, with particular recognition of the needs of the rural poor, yet arrangements and mechanisms remain unclear. Notions of equity within REDD policy proposals are often inconsistent. Prevailing ideas focus on market-based benefit distribution, which is less likely to serve the interests of poor and indigenous peoples.
Crashing carbon market	Finally, there are concerns by some environmental groups that allowing large volumes of REDD credits to be traded in the compliance market would drive carbon prices down and crash the market.

1.3. Methods for measuring above-ground biomass and carbon stocks

In the following paragraphs, three different methods for estimating above-ground biomass are described. In particular, the field-based method is discussed in more detail as this method will be used for this research project. First, the relation between above-ground biomass and carbon stocks is discussed.

1.3.1. Above-Ground Biomass (AGB) and carbon stocks

The majority of the carbon stored in tropical forest ecosystems is found in the living biomass of trees, woody debris, dead ground litter and soil organic matter. Among these different forest components, the above-ground biomass (AGB) of living trees contains the largest carbon pool and is the most directly affected by deforestation and degradation activities (Gibbs et al., 2007). Consequently, measurements of the carbon stored within the AGB of living trees provide the most representative estimate of the forest carbon stocks for REDD.

It has generally been assumed that the carbon content of the AGB of living trees consists of 50% of overall biomass (Clark et al., 2001; Lamtom & Savidge, 2003). However, other studies have argued that the carbon content of AGB can vary between 47% and 59% depending on the tree species (Ragland et al., 1991; Elias & Potvin, 2003; Lamtom & Savidge, 2003). Species may differ in carbon content due to their unique chemical composition and anatomy, and therefore in specific wood density. Furthermore, the Intergovernmental Panel on Climate Change (IPCC) decided to use a carbon fraction of 0.47 of biomass in its calculations (Gibbs et al., 2007). Due to

the potential variation in the carbon content of the AGB of living trees, the results obtained in this study are not converted into carbon values but kept as initial AGB values. This decision also makes comparison with the results of other studies more straightforward because they are most commonly presented in this form.

1.3.2. The biome-average approach

The biome-average approach estimates forest carbon stocks by applying a specific representative value of forest carbon per unit area (i.e. tonnes of C per hectare) to large forest categories or biomes (Fearnside, 2000; Gibbs et al., 2007). These biome averages are based on two main data sources. One source is the compilations of biomass harvest measurement data: all trees in a defined area are harvested, dried and weighed to measure their biomass. Although this approach produces very accurate results for a specific site, it is very time-consuming, expensive, destructive and highly biased for extrapolation over a larger spatial scale such as country level (Gibbs et al., 2007). The other source of data for the biome-average method makes use of forest inventory data gathered by the Food and Agriculture Organization (FAO) and others. However, the data from forest inventories are missing a lot of information for tropical forests and tend to be collected inadequately for conclusions to be made on a national level (FAO, 2005; Gibbs et al., 2007).

Despite the limitations and uncertainties of the biome-average approach, it still remains a regularly used method for estimating forest carbon stocks because it is free, easily accessible and is considered as an important source for global carbon information (Gibbs et al., 2007). However, more recent methods are developing which may provide better estimates of forest carbon stocks across a larger spatial scale.

1.3.3. Field-based method and allometric equations

Sampling method for collecting field data

The first step for the field-based approach is to collect field data using standardized sampling methods with appropriate plot size, shape and number in order to generate accurate biomass estimates. The most commonly used sampling method for forest inventories is based on 1 hectare square plots as suggested by the FAO (Baraloto et al., in review). However, other studies have argued that this type of plot design may not actually be adequate for characterizing carbon stocks and fluxes (Wagner et al., 2010; Keller et al., 2001). For example, Keller et al. (2001) carried out their research in the Tapajos National Park in Brazil and found that 21 plots of 0.25 hectares each were sufficient to make estimates of mean biomass. Their results were within only a 20% error sampling and 95% confidence. In turn, several methods have been suggested to improve either the accuracy of the results and/or its efficiency (amount of effort required for data sampling).

Allometric equations for calculating AGB

The second step of the field-based method is to convert field data into an estimate of AGB by applying allometric regression models, also referred to as allometric equations. In other words, the field measurements provide the parameters necessary to calculate AGB using allometric equations such as measurements of Diameter at Breast Height (DBH) and/or tree height. These allometric equations are developed by using a large dataset from harvested trees which means that it is relatively time-consuming, expensive and destructive to develop (Gibbs et al., 2007). Generalized allometric equations for different forest types are developed rather than species-specific allometric equations because tropical forests can generally contain over 300 different species in a 1 hectare plot (Chave et al., 2005). Furthermore, studies have shown that generalized allometric equations for different forest types generate accurate estimates of AGB

and that efforts made to develop species or site specific regression models do not systematically improve its accuracy (Chambers et al., 2001; Keller et al., 2001; Chave et al., 2005; Gibbs et al., 2007). It must be emphasized that specific allometric equations for each regional forest type provides more reliable AGB results than one grouped allometric equation for all forest types. Therefore, regional forest type is an important factor to be taken into consideration when calculating forest AGB. These regional forest types are classified with regards to their mean annual rainfall, dry season length and evapotranspiration activities (Chave et al., 2005).

Several different allometric equations have been developed for tropical forests and the most well-known are by Brown et al. (1989), Chambers et al. (2001), Chave et al. (2001) and Chave et al. (2005). Applying these different equations for the same studied forest area can yield different AGB estimates. The quality of the AGB outcomes obtained from the allometric equations will depend on the data used to create them as well as the range of parameters included. For an allometric equation to be representative of a forest area, it needs to be based on a large number of trees harvested as well as a large number of big diameter trees (Brown et al., 1989; Chave et al., 2005). Moreover, in general the more parameters from field measurements included into the allometric equation, the more accurate the AGB results. Allometric equations can make use of one or more of the following parameters: DBH, tree height and species specific wood density.

Country-level forest carbon stocks

Once the allometric equation has been applied to the field measurements, estimates of the average AGB and ultimately average carbon stocks for each regional forest type can be determined. Consequently, a country's forest carbon stock can be estimated by applying these average carbon stock values across a national land-cover map (Gibbs et al., 2007). Remote sensing methods are often used as a basis for this extrapolation, as discussed in the next section.

1.3.4. Remote-sensing method

The development of new technologies for remote-sensing using satellites or airborne platforms can be viewed as a promising approach for evaluating forest carbon stock (DeFries et al., 2007). Patenaude et al. (2005) describe remote-sensing as a "process of imaging the interactions between electromagnetic energy and matter at selected wavelengths", which has the ability to monitor changes on terrestrial ecosystems over a wide range of temporal and spatial scales. Therefore, remote-sensing can play a valuable role in the assessment of forest carbon stocks for establishing national baselines as well as monitor potential changes due to deforestation or degradation (Rosenqvist et al., 2003). However, much progress and refinement is still needed before regular assessments can be undertaken across such large spatial scales (DeFries et al., 2007; Gibbs et al., 2007). Furthermore, no remote-sensing technique can yet directly measure forest carbon stocks and so still require supplementary field-based data and field-derived allometric relationships in order to generate accurate AGB or carbon estimates (Drake et al., 2003; Gibbs et al., 2007).

1.4. Main factors influencing the variation in above-ground biomass

To select and apply an appropriate method is a crucial step for accurately estimating forest AGB. In addition, understanding and identifying the main causes for changes or differences in forest AGB over temporal and spatial scales is also an essential aspect for improving AGB estimates. Two important factors explaining the variation in forest AGB are the environmental factors driving AGB spatial patterns and human induced disturbances, in particular logging activities. These factors are discussed in further detail in the following paragraphs.

1.4.1. Environmental factors driving spatial variation in AGB

Several studies have determined spatial variation in forest biomass on global and regional scales. For example, Slik et al. (2010) have evaluated that the average AGB of Borneo's forest was 457.1 Mg/ha which is approximately 60% greater than the estimated AGB within the Amazonian forest of 288.6 Mg/ha. Furthermore even across the Amazon basin, several studies have reported spatial patterns in AGB along an east-west geographic gradient, with central and eastern forests having higher overall AGB estimates than in northwest or southwest Amazonia (Baker et al., 2004a; Malhi et al., 2006; Quesada et al., 2009; Baraloto et al., 2011).

Although some apparent global and regional variation in AGB (Malhi et al., 2006; Slik et al., 2010) have been highlighted, there is no general agreement on the relative importance of the different environmental factors causing these observed variation in AGB. So far the only studied environmental factor demonstrating a consistent positive relationship with AGB is linked to climate as regions with high rainfall distributed evenly throughout the year appear to support the highest forest biomass such as in Panama, the Amazon and Borneo (Saatchi et al., 2007; Malhi et al., 2006; Slik et al., 2010). More specifically, the strongest relationship occurs during the dry season which supports the findings that biomass production depends especially on water availability throughout the dry season during which light and radiation are abundant (Saleska et al., 2003; Malhi et al., 2006; Saatchi et al., 2007). On the other hand, conflicting results have been put forward by different studies about the relationship between AGB and soil type (chemical and physical properties) or topography. A few studies have reported a positive effect of nutrient-rich fertile soils on AGB (Castilho et al., 2006; Paoli et al., 2008; Slik et al., 2010) which suggests that AGB may be limited by soil nutrient availability. Meanwhile other researchers have stated that soil fertility has no effect (Clark & Clark, 2000; Chave et al., 2003) or even negative effects (Van Schaik & Mirmanto, 1985; Quesada et al., 2009) on forest biomass because of the high turnover rates on fertile soils, resulting in lower standing stocks.

Apart from environmental factors related to climate and soil, studies have also focused their attention on the influence of forest structure and composition on AGB estimates, which can also be referred to as stand variables. In general, it would be expected for stand variables to be important positive correlates for AGB, especially those variables used in the allometric equations such as diameter, height and wood density (Chave et al., 2005). However, Stegen et al. (2009) argued that there is no general relationship between AGB and mean community wood density and they even occasionally found highest biomass values within forests of low wood density. Nonetheless, more conclusive results have underlined the importance of stem density and basal area for driving spatial variation in AGB estimates (Rutishauser et al., 2010; Slik et al., 2010). Finally, the general conclusions from the literature about the different environmental factors explaining regional spatial variation in forest biomass are summarized in Table 2, page 17 (Baraloto et al., 2011).

Table 2. A summary of the effects of the three main categories of environmental factors (climate, soil and stand variables) on the above-ground biomass in tropical forests. The sign ‘+’ represents a positive relationship, ‘-’ a negative relationship and ‘*’ conflicting results.

Source: Baraloto et al. (2011).

Group	Factor	Effect	References
Climate	Total Precipitation	+	Malhi <i>et al.</i> (2006); Chave <i>et al.</i> (2004)
	Dry season length	–	Malhi <i>et al.</i> (2006); Chave <i>et al.</i> (2004)
Soil	Topography	*	Clark & Clark (2000); Ferry <i>et al.</i> (2010)
	Texture	*	Paoli <i>et al.</i> (2008); Quesada <i>et al.</i> (2009)
	Exchangeable bases	*	Laurance <i>et al.</i> (1999); Quesada <i>et al.</i> (2009)
	Labile P	*	Paoli <i>et al.</i> (2008); Quesada <i>et al.</i> (2009)
	Type	*	DeWalt & Chave (2004)
Stand	Basal area	+	Baker <i>et al.</i> (2004); Malhi <i>et al.</i> (2006); Paoli <i>et al.</i> (2008)
	Density of large trees	+	DeWalt & Chave (2004); Paoli <i>et al.</i> (2008); Rutishauser <i>et al.</i> (2010)
	Mean Tree Height	+	Chave <i>et al.</i> (2005)
	Mean Tree DBH	+	Nelson <i>et al.</i> (1999); Chave <i>et al.</i> (2005)
	Mean Wood specific gravity	*	Baker <i>et al.</i> (2004); DeWalt & Chave (2004); Stegen <i>et al.</i> (2009)

1.4.2. Logging activities driving temporal variation in AGB

Logging refers to a broad range of forestry activities involving wood harvesting. Logging activities have a direct impact on forest biomass as part of the felled trees are removed from the forests meanwhile the rest are left to decompose. The removed harvested wood can either be used to manufacture commercial products or to produce energy (Liski et al., 2001). After manufacture, it is estimated that only one-third of the harvested biomass ends up in the final wood product due to poor sawmill transformation efficiency and specific requirements imposed for the final product (Blanc et al., 2009). The carbon contained in the wood product is expected to stay “locked” inside for a long time period since hardwood products tend to have a long life cycle. On the other hand, the other two-thirds of unused forest biomass are generally burned, resulting in immediate carbon emissions into the atmosphere (Keller et al., 2004). In the same way, the use of biomass to produce energy also leads to immediate carbon emissions as it is generally used for cooking and heating in most developing countries (Field et al., 2008).

Logging also generates indirect changes in forest biomass because it causes damage to the remaining forest during felling, skidding or the transportation of harvested wood. The intensity of the damage will depend on the type of logging activity carried out: conventional, selective or reduced impact logging. Under selective logging, a restricted number of marketable tree species and of defined minimum diameter are targeted (Asner et al., 2005). Moreover, conventional or traditional logging practices make little or no efforts to prevent forest damage. For example, about 40-70% of the remaining trees left after conventional selective logging in Sabah, Malaysia, were damaged. For an additional; 17-30% of the harvested area damage was also reported after the passage of bulldozers (Healey et al., 2000). This damage to the remaining forests will have consequences for forest dynamics and structure, ultimately leading to changes in AGB over time. In particular, three factors of forest dynamics will influence AGB accumulation after logging: recruitment, growth and mortality. Blanc et al. (2009) carried out a study in French Guiana and their findings showed that after an initial period of high mortality increase, mortality rates remained still ~30% higher for about 8 years after logging in comparison to before logging. Therefore, the mortality of damaged trees is likely to have a negative effect on the AGB for several years after logging. The time required for forest biomass to recover after logging activity is likely to depend on the intensity and extent of the damage occurred.

Over the past two decades, forest harvesting guidelines have been developed for the purpose of reducing the negative environmental impact of logging activities and are referred to as reduced-impact logging (RIL) techniques. RIL can be defined as “intensively planned and carefully controlled timber harvesting conducted by trained workers in ways that minimize the

deleterious impacts of logging” (Putz et al., 2008). The implementation of RIL instead of traditional logging practices is considered to prevent about 50% or more of forest damage, thereby more AGB is maintained intact within the residual forest (Putz et al., 2008). Due to the low damage, it is expected that the residual forest after RIL will be able to recover faster than after conventional logging (Pinard & Putz, 1996). Therefore, higher AGB increments are to be expected in RIL areas than CL areas.

1.5. Research project in French Guiana

The overarching aims of this research project are to study in French Guiana:

- 1) *the effects of selective logging activity on forest above-ground biomass*
- 2) *the spatial variation in above-ground biomass of primary forests*

To address these two aims, differences in forest AGB over spatial and temporal scales in French Guiana are examined. The objective of this study is to provide further insight in sources of variation in forest AGB in French Guiana, which is essential for improving the accuracy of AGB estimates required for future REDD+ planning and implementation. Due to its large primary forest cover, French Guiana has been ranked as containing the 2nd highest national forest carbon stock in South America, with an estimated total carbon stock in living biomass of 1.651 Mt (FAO, 2010). Therefore, French Guiana is a good candidate to qualify for the voluntary carbon market under REDD+ projects. Consequently, this research project seeks to provide a basis for further REDD+ research in the area.

Several studies investigating forest AGB have already been carried out across French Guiana and more specifically in the Kaw Mountains (Ter Steege et al., 2003; Kruijt et al., 2006; Duden & Roeling, 2011). As a result a vast body of data is available for future research on AGB estimates in the area. In particular, the two research centers EcoFoG and CIRAD were willing to share a lot of their data from previous studies on AGB estimates. Therefore for this study, field data was collected in the Kaw Mountains and further data from other forest sites were integrated into the analysis in order to achieve the main aims of this research project.

Finally, there is a risk that the forest in the Kaw Mountains will be subject to increasing pressure because of growing population demands, further encroachment of human settlements, infrastructure development and mining concessions (Kruijt et al., 2006). In consequence, the intention of this research is also to provide further knowledge to promote the conservation of forest carbon stocks in the Kaw Mountains under future REDD+ schemes.

Research questions

The two main aims of the research project will be addressed through the following research questions:

- Is there a significant difference in AGB and forest structure between two primary forest sites in the Kaw Mountains?
- Is there a significant difference in AGB and forest structure between primary and secondary forest sites after recent selective logging in the Kaw Mountains?
- Is there a significant difference in AGB between two secondary forest sites after recent selective logging in the Kaw Mountains and Turtle Mountain?
- Is there a significant difference in AGB between before and after recent selective logging in the Turtle Mountain?

- What are the predicted changes in AGB over the next 50 years for both primary and secondary forests in the Kaw Mountains and Turtle Mountain?
- Can we identify regional spatial patterns in AGB between several primary forest sites across French Guiana?
- What is the relationship between environmental factors with AGB?

2. Methods

2.1. Study area

French Guiana

French Guiana is a French overseas department situated between 2°10' and 5°45'N and 51°40' and 54°30'W in northeastern South America (Chave et al., 2001). It has an extremely high forest cover, with practically 98% of the country's territory dominated by tropical forest which is still largely undisturbed (FAO, 2010; Thoisy et al., 2005). The majority of its forest is composed of lowland wet tropical forest (97%) and an additional small proportion is made up of coastal savannas. Furthermore, French Guiana contains a rich biodiversity with an estimated 5 750 plant species currently known, including 151 endemic species (Gargominy, 2003). Many new species are still frequently being discovered as little research has yet been carried out in many areas. Therefore, there is a high concern for promoting forest conservation in the country under REDD+ projects.

French Guiana has a humid tropical climate and annual rainfall varies between 1650 and 4000mm⁻¹, with highest values near the coastal region and gradually decreasing towards the southern part of the country (Chave et al., 2001). The wet season occurs from December to July, with maximum rainfall reached in May and June. A pronounced dry season occurs from August to December and a short dry season also takes place between March and April (ONF, 1995). French Guiana's geology is typical of the Guiana Shield as it consists of sparse mountains of Precambrian metamorphic and granite rocks (Chave et al., 2001). Finally, the altitude is overall less than 500 meters above sea level.

Kaw Mountains

The Kaw Mountains is located at approximately 45 km from the capital city, Cayenne (see map in Appendix 1). The mountain has a dense forest area. Due to the positioning of the mountain parallel to the coastline, it receives an extremely high amount of rainfall in comparison to other forest sites in French Guiana. The average yearly rainfall is over 4000 mm, with maximum rainfall reaching up to 800 mm on certain high points of the mountain (Ek et al., 2000).

The departmental road D6 crosses the Kaw Mountains. Although, no communities are living on the mountain itself, several tourism and exploitation activities are present. The ONF possesses many parcels in the area, which are used from logging activity. In addition, two nature reserves have also been established: Marais de Kaw and the Regional Nature Reserve of Trésor.

Trésor Nature Reserve (Réserve Naturelle Régionale Trésor)

The Trésor Foundation was founded in 1995 under the initiative of Utrecht University. The Foundation acquired about 2464 ha of tropical forest located at the south-facing slope of the Kaw Mountains (Ek et al., 2004). It received the official status to become a nature reserve in 1997 (Sluiter et al., 2006). For the Trésor regional nature reserve, it is of interest to explore the potential value of the reserve regarding the carbon stored in its AGB, in order to broaden the basis for maintaining the reserve (Kruijt et al., 2006).

Furthermore, this nature reserve is home to a great variety of flora and fauna species. Floristic inventories carried out in the Trésor area have identified up to 1233 plant species (Ek et al., 2006). Since investigations in the reserve are relatively recent, many new species are still to be discovered and identified. Furthermore, Ek et al. (2000) distinguished seven different vegetation types in the Trésor area based on species composition, topography, forest physiognomy and soil type (see Figure 2). For this research project, the biomass present in the 'mountaintop' forest type was studied. This mountaintop forest is characterized by a Terra Firme forest which grows on a lateritic plateau covered by a thin layer of fertile soil (Trésor Foundation website, 2011).

The water availability is low due to the low water storage capacity of the thin upper soil layer. This is especially an issue during the dry season for the undergrowth plant species that root only on the thin soil layer. As a result, there is little undergrowth species present on the mountaintop forest type. However, many trees of different age and size classes are present due to the high turnover rate in this forest type (Trésor Foundation website, 2011).

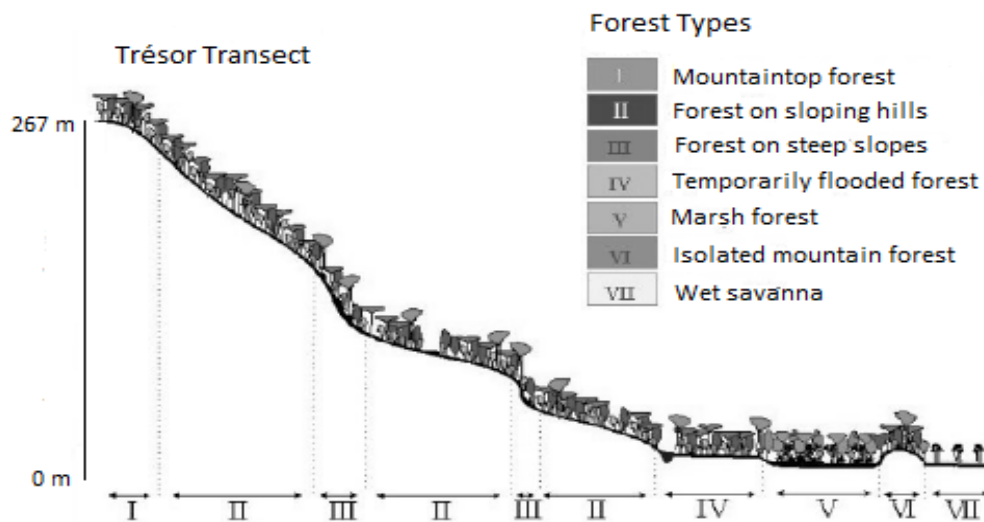


Figure 2. Modified figure from Ek et al. (2000) representing the seven different vegetation types present in the Trésor nature reserve.

ONF forest area

The National Forestry Office (Office National des Forêts, ONF) is responsible for the surveillance, management and exploitation of practically 5.5 million hectares of public forest in French Guiana (ONF website, 2011). More specifically, ONF manages forest areas in both the Kaw Mountains and Turtle Mountain. The forests areas are divided into protected and non-protected zones by ONF. In the non-protected zones logging activity is permitted. In the Kaw Mountains, the “Zwahlen” company has been exploiting several plots for over the past 25 years. The type of logging being carried out by ONF is considered as selective logging since only certain tree species are being targeted. However, the species logged depend on market demands and therefore can change accordingly. Among the 50 different species labeled as marketable by the CIRAD organization, only 15 species are frequently exploited (ONF, 1995). In particular, 3 species make up 2/3 of the logged volume: Gonfolo (*Qualea spp.*), Angélique (*Dicorynia guianensis*) and Grignon franc (*Sextonia rubra*; ONF, 1995). In French Guiana, the total amount of forest loss due to logging activities in the country is relatively low, with an estimated 0.4% per year over 2005-2010 (FAO, 2010). Moreover, the mean logging intensity is 14m³/ha with maximum logging never exceeding 43m³/ha (Gourlet-Fleury et al., 2004; Blanc et al., 2009). The cutting cycles in French Guiana are currently set at 65 years whereas in most neighboring countries cutting cycles of less than 30 years tend to be applied (Blanc et al., 2009). These fixed cutting cycles are meant to let the forest regenerate before potential re-exploitation. Finally in this study, field data was collected in the protected and non-protected ONF forest area in the Kaw Mountains. The non-protected forest area was logged by ONF in 2006, resulting in a total volume of 1872.43 m³ of wood extracted.

2.2. Field-based method

To address the research questions, field work was carried out in the Trésor Nature Reserve (Réserve Naturelle Régionale Trésor) and the ONF forest area in the Kaw Mountains.

2.2.1. Sampling approach

Gentry Plots

Field data was collected using the 0.5-ha modified Gentry plot method (Figure 3, page 23; Baraloto et al., 2011), which will be referred to as Gentry plots from now on. This sampling method is considered to be the most efficient for providing accurate AGB and biodiversity estimates as demonstrated by Baraloto et al. (in review). They compared five commonly used sampling methods to estimate AGB as well as tree diversity across six Neotropical forest types varying in structure and floristic composition. Their findings suggest that in general, more accurate estimates of AGB are obtained with multiple smaller plots than fewer larger plots. More specifically, they found that the Gentry plot method performed better than the other methods in providing both accurate AGB and biodiversity estimates. Furthermore, this method was found to be the most efficient for estimating AGB across the different forest types as it required less effort than smaller size plots to attain accurate estimates. In addition, about 160 Gentry plots are currently set up in Peru, Bolivia, French Guiana, Suriname and Brazil. This enables for comparison using a large database from different sites obtained using the same standardized method. In consequence, the Gentry plot method was used in this study to collect field data.

As illustrated in Figure 3, the Gentry plot method consists of a transect baseline of 190 m long and a set of ten rectangular subplots of 10 x 50 m (resulting in a total plot surface of 0.5 ha) which are oriented in alternative perpendicular directions to this baseline. Therefore, five subplots are laid out along each side of the baseline with 20 m separation between the midline of each subplot. Within these subplots, all woody stems of DBH greater than 10 cm were sampled. These field measurements were used to study forest biomass, thus these subplots will be referred to as “10 meters forest subplots”. For a rapid and accurate assessment of biodiversity, all woody stems of DBH greater than 2.5 cm were sampled within ten 2 x 50 meters subplots situated along the midline of each of the 10 meters forest subplots. These smaller sized transects will be referred to as “2 meters botanic subplots”..

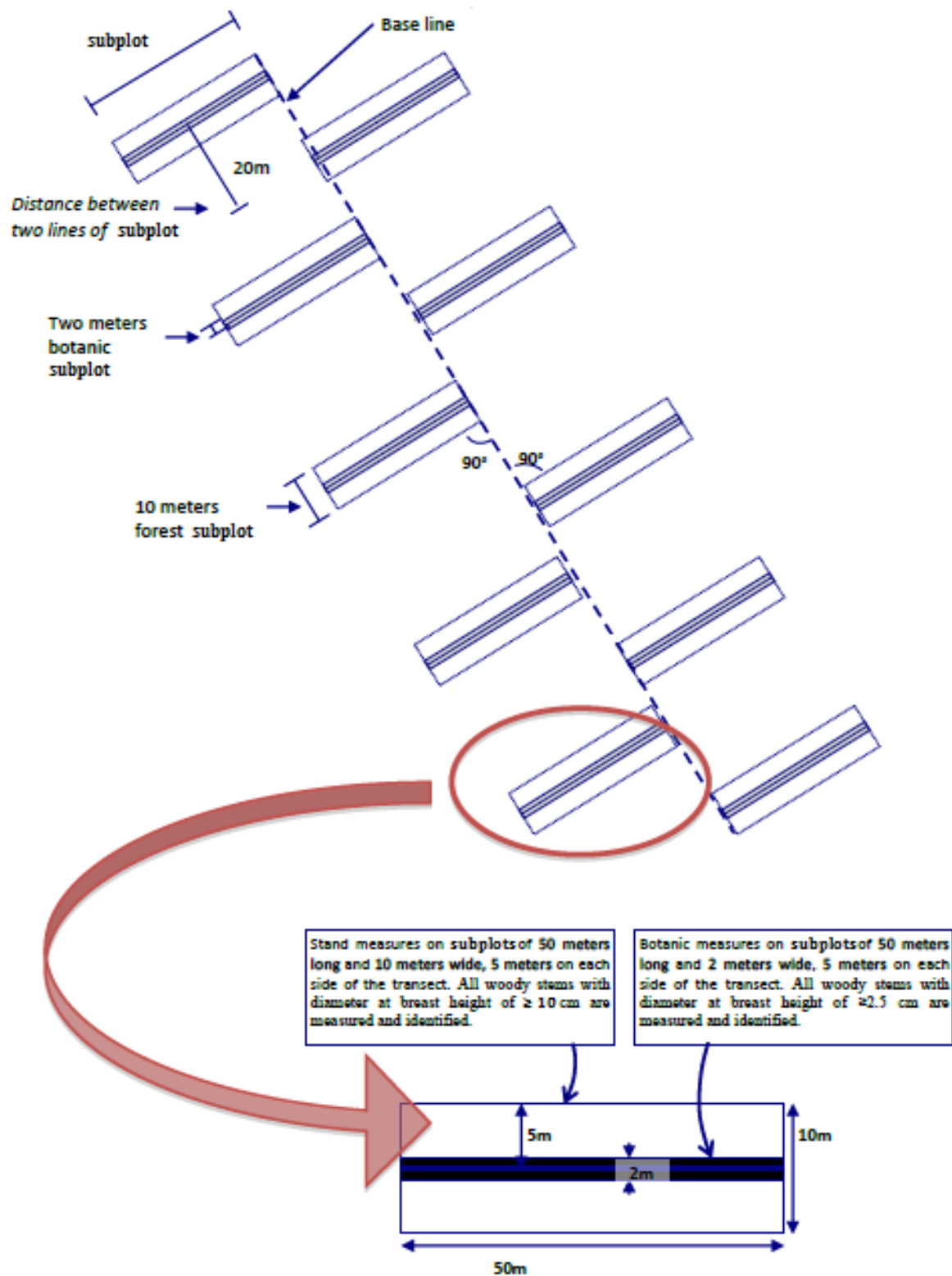


Figure 3. The layout of the 0.5-ha modified Gentry plots. Source: Baraloto et al. (2011).

A total of 9 Gentry plots were established in the Kaw Mountains. The criteria for selecting plot locations were:

- Mountaintop Terra Firme forest type
- Flat areas, no steep slope present
- Homogeneous forest within at least 100 m x 190 m surface area
- Accessibility
- Land use (logged or unexploited forest)

From these 9 Gentry plots, data from 3 Gentry plots were already collected during a previous research project in the Kaw Mountains by Duden & Roeling (2011). In this study, an additional 6 Gentry plots were carried out in the forest area while taking into consideration that sufficient replicates were gathered for data analysis. Therefore, the total 9 Gentry plots were set out as followed:

- 3 Gentry plots in the primary forest of the Trésor nature reserve
- 3 Gentry plots in the primary forest of ONF
- 3 Gentry plots in the secondary forest of ONF that had been logged 5 years before

Before setting the Gentry plots, the locations were first checked during field surveys with experts from the Trésor Association, ONF, CIRAD and EcoFoG. Due to the nature of selective logging, logging activity tends to be not uniform over the entire exploited area. To make sure that Gentry plots in the secondary forest of ONF were located in areas that had been previously exploited, the baseline was placed along the leftover tracks made by the heavy forestry machinery. In addition, the number of stumps inside the sampled area was recorded in order to have an idea of the logging intensity in the area.

The locations of the baseline of these 9 Gentry plots in the Kaw Mountains are shown in Figure 4. From this map, one Gentry plot situated in the Trésor reserve is laid out differently. This Gentry plot was modified because it is placed very close to the road in order to study potential edge effects on carbon stocks (Duden & Roeling, 2011). Thus for our study, the two first initial subplots situated close to the road were replaced by two subplots located on each side of the main baseline, in order to avoid this potential edge effect.

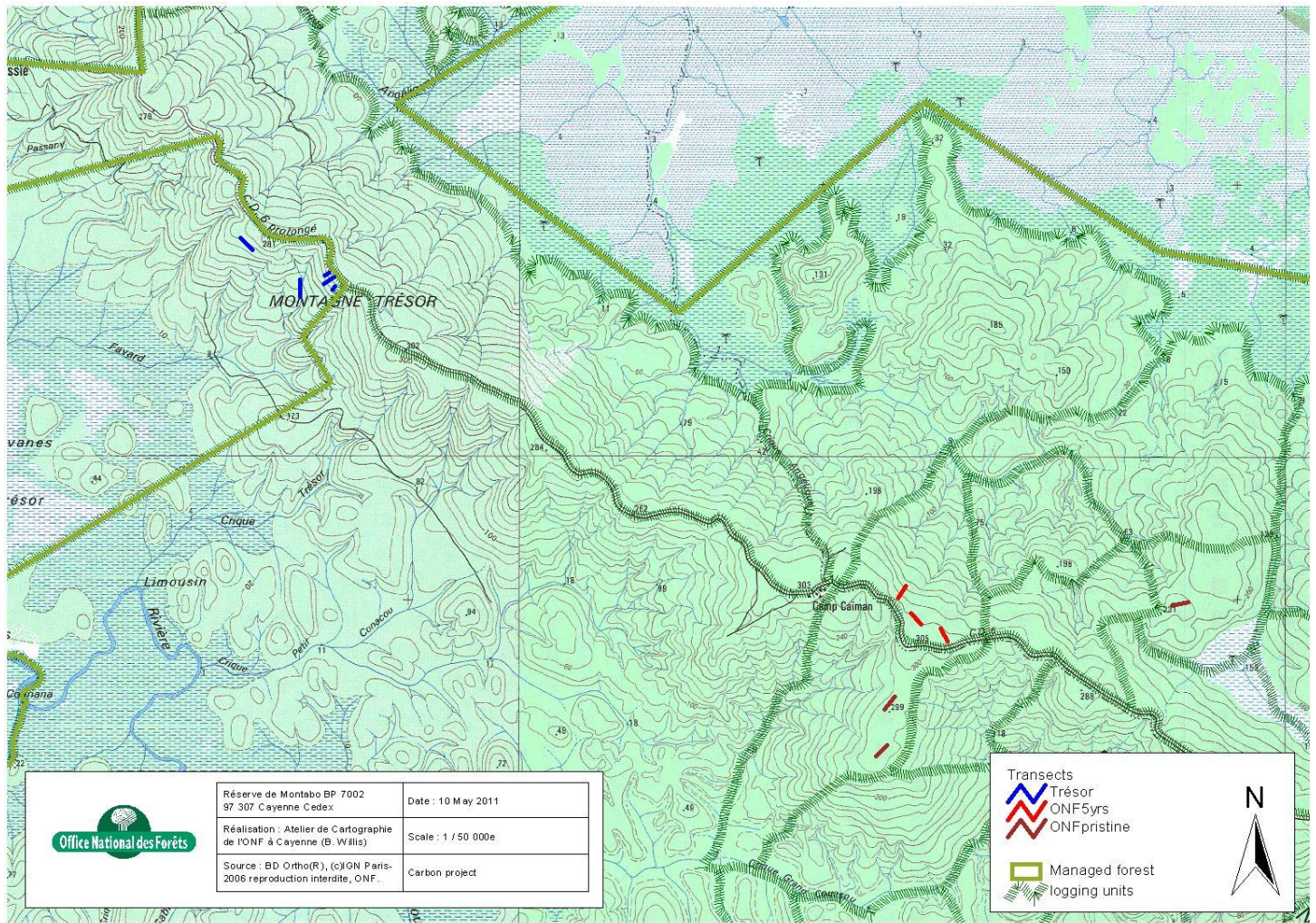


Figure 4. Map showing the location of the baseline of the 9 Gentry plots in the Kaw Mountains. The Gentry plots situated in the primary forest of Trésor, secondary forest of ONF and primary forest of ONF are represented in blue, red and brown respectively. This map was created using GIS ArcView program.

Field Measurements

Within the 10 meters forest subplots, field measurements were carried out for all trees and lianas with a DBH greater than 10 cm. Meanwhile within the 2 meters botanic subplots, trees and lianas with a DBH greater than 2.5 cm were sampled. The trees and lianas were considered as being inside the subplot if the center of their trunk at soil surface was located within the limits of the subplot. For trees, both DBH and height was measured whereas for lianas only DBH was measured as its height/length is extremely difficult to estimate due to its irregular shape. DBH is a standard dendrometric measurement used to determine the diameter of a tree at 1.30 meters from the ground using measuring tape. However for trees with buttress roots, diameter was measured above the buttress roots when possible in order to have a more representative diameter for the entire tree trunk. If that was not possible, diameters of neighboring trees were used as references. Tree height was defined as the length from the base of the trunk to the highest leaf. Height was measured using a hypsometer (Nikon 550 Forestry Rangefinder). This laser device calculates tree height by measuring the distance of the observer to the tree, the distance from the observer to the top of the tree and the angle between these two measured distances.

Furthermore within the 10 meters forest subplot, the DBH and height/length of dead standing trees and fallen dead trees were also measured. For dead fallen trees, only the length of the trunk lying inside the subplot was measured.

Within each 10 meters forest subplots, all measured living trees, dead trees and lianas were given an x and y coordinate, and were labeled and spray painted at the point of measurement for DBH. By labeling and giving x and y coordinates, it will facilitate future research to easily recognize these already measured trees and lianas. Furthermore, labeling was practical to receive additional information on tree species. After field measurements in the 10 meters forest subplots, two tree specialists from CIRAD would identify the tree species of all labeled trees. With the information on tree species, their wood density can be determined using a global wood density database (Chave et al., 2005).

Furthermore, all the trees in the 2 meters botanic subplot with a DBH greater than 2.5 cm were measured and identified in order to provide further information about the forest structure and the contribution of the AGB of small living trees to total AGB.

2.2.2. Allometric equations for AGB calculations

The AGB of living trees, dead trees and lianas were calculated using different allometric equations, each described in Table 3, page 27. The allometric equation developed by Baker et al. (2007) was used to estimate the AGB of standing and fallen dead trees. For this equation, they classified the state of decomposition of dead trees into five categories. In this study, the decomposition class number 3 was applied to estimate the AGB of all the dead trees encountered inside the Gentry plots as it can be considered the most general representative state. Dead trees belonging to the decomposition class number 3 are defined as “non-solid wood, in poorer condition, but where it was still difficult to push a nail into the wood by hand” (Baker et al., 2007). For lianas, AGB calculations were made using the equation of Schnitzer et al. (2006). This recent allometric equation for lianas was developed from a large dataset of 424 lianas collected in four different countries.

Finally, to calculate living trees AGB, the generalized allometric equation for the pan-tropics developed by Chave et al. (2005) was used. This allometric equation is currently considered as the most reliable and robust model to estimate AGB across a broad range of tropical forest types because it has been based on exceptionally large database of 2410 trees, directly harvested in 27 study sites across the tropics. This allometric equation also includes all three parameters: DBH, height and species specific wood density. However, if a species was unknown, the average wood density for the Gentry plot would be included instead into the equation.

Furthermore, to have an idea of how the different parameters included in the Chave et al (2005) equation may affect the biomass results obtained, AGB was also calculated using the equation from Chave et al. (2005) without height (modified equation) and/or with only the mean wood density for the whole Gentry plot instead of the specific wood density for all known species. In Appendix 2, the AGB estimates for each Gentry plot using the different equations is represented in a graph. This graph shows that when excluding height from the equation, AGB tends to be overestimated. In addition, the AGB estimates obtained were slightly underestimated when including only a mean wood density (abbreviated as wsg in legend) for each Gentry plot instead of using specific wood densities for all identified species. These findings are similar to what has been reported by other studies. For example, Baraloto et al. (2011) found that AGB estimates were always greater when height was not integrated into the allometric equation and this bias was even greater in plots with higher AGB. In consequence, AGB calculations in this study used the Chave et al. (2005) allometric equation which includes the following parameters: DBH, height and species specific wood density.

Table 3. Overview of the different allometric equations used to calculate AGB in this study. For all allometric equations: Above-ground Biomass (AGB) is in kg, Diameter at Breast Height (DBH) is in cm, Height (H) is in m, Wood density (WSG) is g/cm³.

Type of AGB	Allometric equation (AGB in kilograms)	Source	Extra information
Dead trees	$AGB = 0.0509 \times (0.4 \times DBH^2 \times H) \times 0.5$	Baker et al. (2007)	Formula for a Class 3 state of decomposition
Lianas	$AGB = e(-1.484 + 2.657 \times \ln(DBH))$	Schnitzer et al. (2006)	
Living trees	$AGB = 0.0509 \times WSG \times DBH^2 \times H$	Chave et al. (2005)	Formula including height
Living trees	$AGB = WSG \times e(-1.499 + 2.148 \times \log(DBH) + 0.207 \times \log(DBH)^2 - 0.0281 \times \log(DBH)^3)$	Modified Chave et al. (2005)	Formula without height

2.3. Data analysis

Data preparation, AGB calculations and statistical analyses were all conducted using the R language and environment for statistical computing version 2.13.0. (R Core Development Team, 2011). A summary of the R script used for AGB calculations is included in Appendix 9.

2.3.1. Selective logging effect and local spatial variation in AGB and forest structure in the Kaw Mountains

The AGB results for the three different forest sites (primary forest in Trésor, primary forest in ONF area and secondary forest in ONF area) were presented in a histogram, table and boxplot. An ANOVA analysis was carried out to study if there were any significant differences in total AGB between the three different forest sites. The ANOVA was carried out by using the three replicates of the Gentry plots for each forest site. Furthermore, ANOVA analyses were also carried out to test in more detail for AGB differences among small living trees (DBH ≤ 10 cm), big living trees (DBH ≥ 10 cm), dead trees and lianas.

To study the forest structure, the stem density (number of trees/hectare) and basal area (m²/hectare) between the different forest sites were compared. To determine if there were any significant differences, an ANOVA analysis was carried out. Furthermore, the distribution of trees within different DBH size categories was also studied. The DBH categories were defined in order to get as much information as possible about the forest structure while also making sure that a minimum of 5 counts were present in each category to obtain reliable results from the data analysis. A Pearson's Chi-square test was used to assess if logging and/or local spatial variation had an effect on DBH-class distributions. To obtain further information about differences in DBH-classes, the standardized residuals obtained from the Chi-square test were examined. Furthermore, histograms were produced to compare the distribution of the percentage of AGB and number of trees within the different DBH classes for the three forest sites.

2.3.2. Temporal variation in AGB due to selective logging activity in the Turtle Mountain and the Kaw Mountains

A long-term research project to study the changes in AGB over time due to logging activity in the Turtle Mountain (see map in Appendix 1) has been established by the research centers CIRAD and EcoFoG. Selective logging activity was carried out in 2005 within designated plots. The intensity of the logging activity in the Turtle Mountain is similar to the logging activity carried

out by ONF in the Kaw Mountains: 4 to 6 stems per hectare. So far, the research centers of CIRAD and EcoFoG have collected data to obtain AGB estimates in the Turtle Mountain in 2002, 2007 and 2010. Therefore, estimates of AGB are available before logging as well as after logging, with more specifically data for two years and five years after logging occurred. These two research centers agreed to share their AGB data in 2002, 2007 and 2010 from two replicate plots both logged in 2005. In addition, they also shared their data collected in 2002 and 2007 from one control plot in the Turtle Mountain (where no logging activity occurred). Moreover, CIRAD and EcoFoG collected data only from big living trees with a DBH equal or greater than 10 cm and AGB estimates were calculated using the allometric equation from Chave et al (2005). In Appendix 3, AGB values in the Turtle Mountain estimated by CIRAD and EcoFoG are presented in a table.

To study the changes in AGB before and after selective logging in the Turtle Mountain, the AGB data from the two logged plots as well as the control plot were represented in a scatter plot graph. A segmented regression analysis was carried out on the AGB data from the logged plots in order to analyse in greater detail the changes in AGB between 2002 to 2007 and 2007 to 2010. Through this approach, two regression lines were fitted and tested for significance. The results of the segmented regressions analysis were summarized in a table. In addition, an ANOVA analysis was also performed on the AGB data from the two logged plots in order to determine if there is a significant difference between 2002, 2007 and 2010. Due to the lack of any replicates, no statistical analysis was carried out on the AGB data of the control plot. Therefore, differences in AGB between the logged and unlogged plots were interpreted from the scatter plot graph but were not tested statistically. Furthermore, a regression line was also fitted on the AGB data from the control plot to study the changes in AGB in a primary forest site.

In consequence, for both the Turtle Mountain and the Kaw Mountains (ONF secondary forest), AGB estimates have been calculated for five years after logging occurred. The secondary forest areas studied in the Kaw Mountains and Turtle Mountain consist of the same forest type: Terra Firme forest. In addition, they were subject to the same intensity of logging activity. Therefore, statistical analysis was carried out in order to determine if there is any significant difference between the mean AGB in these two secondary forest sites. First, a boxplot was produced to compare the AGB values in the two forest sites. Secondly, a t-test analysis was performed in order to determine if there is any significant difference between the mean AGB in these two forest sites.

Finally, the potential changes in mean AGB over the next 10 to 50 years were studied for both the primary and secondary forests in the Turtle and Kaw Mountains. Due to the lack of replicates in the dataset, the predictions of the AGB changes over time were based on the rate of AGB accumulation estimated by Mazzei et al. (2010). They studied the changes in AGB (2004-2008) of 17 plots in Terra Firme forests in the Eastern Amazon (Brazil, Paragominas) after selective logging occurred. As explained earlier in the introduction, the mortality of damaged trees is likely to have a negative effect on the AGB for a few years after logging (Blanc et al., 2009). Mazzei et al. (2010) found that after this initial decrease in AGB post-logging, the average net AGB accumulation in the logged plots was 2.6 Mg/ha/yr. Furthermore, they also estimated the rate of AGB accumulation of unlogged plots in the area between 2004 and 2008, 1.4 Mg/ha/yr. Therefore, these rates of AGB accumulation estimated by Mazzei et al. (2010) were applied to the AGB data of the primary and secondary forests in the Kaw and Turtle Mountains, and the predicted mean AGB values were compared.

2.3.3. Regional spatial variation in AGB across French Guiana

CIRAD and EcoFoG have carried out research to estimate the AGB, using the same Gentry plot method and allometric equation from Chave et al. (2005), in several primary forests throughout French Guiana: Laussat, Nouragues, Regina and Trinité (see map in Appendix 1). All four forest

sites have the same forest habitat as the studied forest in the Kaw Mountains since they are all composed of Terra Firme forest. Therefore, to assess the regional spatial variation in AGB between different primary forest sites in French Guiana, the AGB estimates from CIRAD and EcoFoG along with the AGB estimates obtained in the primary forest in the Kaw Mountains were all compared.

CIRAD and EcoFoG have carried out 6 or 7 Gentry plot replicates in the four primary forest sites (Laussat, Nouragues, Regina and Trinité). As presented in the results section, no significant differences in AGB were found between the primary forest sites in the Trésor nature reserve and the ONF area in the Kaw Mountains. Thus, the 3 Gentry plot replicates in each primary forest were combined in order to have a total of 6 Gentry plot replicates in the primary forest in the Kaw Mountains. Increasing the number of replicates improves the statistical analysis. Moreover for all the different forest sites, only the AGB of big living trees with a DBH greater than 10 cm were compared because dead trees and lianas were not measured previously in the other sites in French Guiana. In addition, small trees with a DBH lower than 10 cm were found to have a low contribution to overall AGB estimates and therefore were not included.

A boxplot was first produced to illustrate the variation in AGB among the five primary forest sites. To study if there are significant differences in mean AGB between the different forest sites, an ANOVA statistical analysis was carried out.

Finally, a Principal Component Analysis (PCA) was also carried on the complete dataset from the different forest sites in order to examine the relationship between climate and stand variables with AGB. The goal of PCA is to identify which combinations of variables explain the largest amount of variation in the dataset. PCA is a powerful tool used in statistics to analyse complex multivariate data.

The variables for each forest site included into the PCA analysis are described in more detail below. It should be taken into account that each variable was treated as being equally important. In other words, each variable was given the same weight in this analysis.

List of the different variables included into the PCA analysis:

- Three categories of AGB variables:
Total AGB, AGB of small stems with DBH between 2.5 cm and 10 cm, and AGB of big stems with DBH of 10 cm and more.
- Seven stand variables (to describe forest structure):
Mean DBH per Gentry plot, mean height per Gentry plot, mean wood density per Gentry plot, basal area per hectare, stem density per hectare for three size classes (number of stems with DBH between 2.5 and 10 cm, number of stems with DBH between 10 and 30 cm, and number of stems with DBH of 30 cm and more)
- Two climatic variables:
Annual precipitation (mm per year) and dry season index (DSI).
CIRAD and EcoFoG have gathered climatic information from the different forest sites using data from Météo France in French Guiana and the meteorological stations nearest to each plot. Rainfall was calculated as a calendar year monthly average and DSI was calculated as the maximum number of consecutive days in each calendar year receiving 10 mm of precipitation (Baraloto et al., 2011).

3. Results

For a clearer interpretation of the results in the next paragraphs, the different size categories of trees are defined as follow: very small trees ($2.5 \text{ cm} \leq \text{DBH} \leq 5 \text{ cm}$), small trees ($\text{DBH} \leq 10 \text{ cm}$), big trees ($\text{DBH} \geq 10 \text{ cm}$), large trees ($\text{DBH} \geq 30 \text{ cm}$), and very large trees ($\text{DBH} \geq 70 \text{ cm}$).

3.1. Selective logging effect and local spatial variation in AGB in the Kaw Mountains

To study the logging effect on AGB, 3 Gentry plots were placed in a secondary forest owned by ONF in the Kaw Mountains (see map in Figure 4, page 25). This forest had been logged five years ago and a total volume of 1872.43 m^3 of wood was extracted over the year 2006. Furthermore to study local spatial variation in AGB in the Kaw Mountains, 3 Gentry plots were established in the primary forest of the Trésor nature reserve and 3 Gentry plots in the primary forest of ONF (see map in Figure 4, page 25).

The mean AGB obtained from the 3 Gentry plot replicates for each forest sites in the Kaw Mountains were compared. The mean AGB results for each forest site are represented in Figure 5 and in Table 4. For additional information, the total mean AGB and associated percentages for the three forest sites combined are given in Appendix 4.

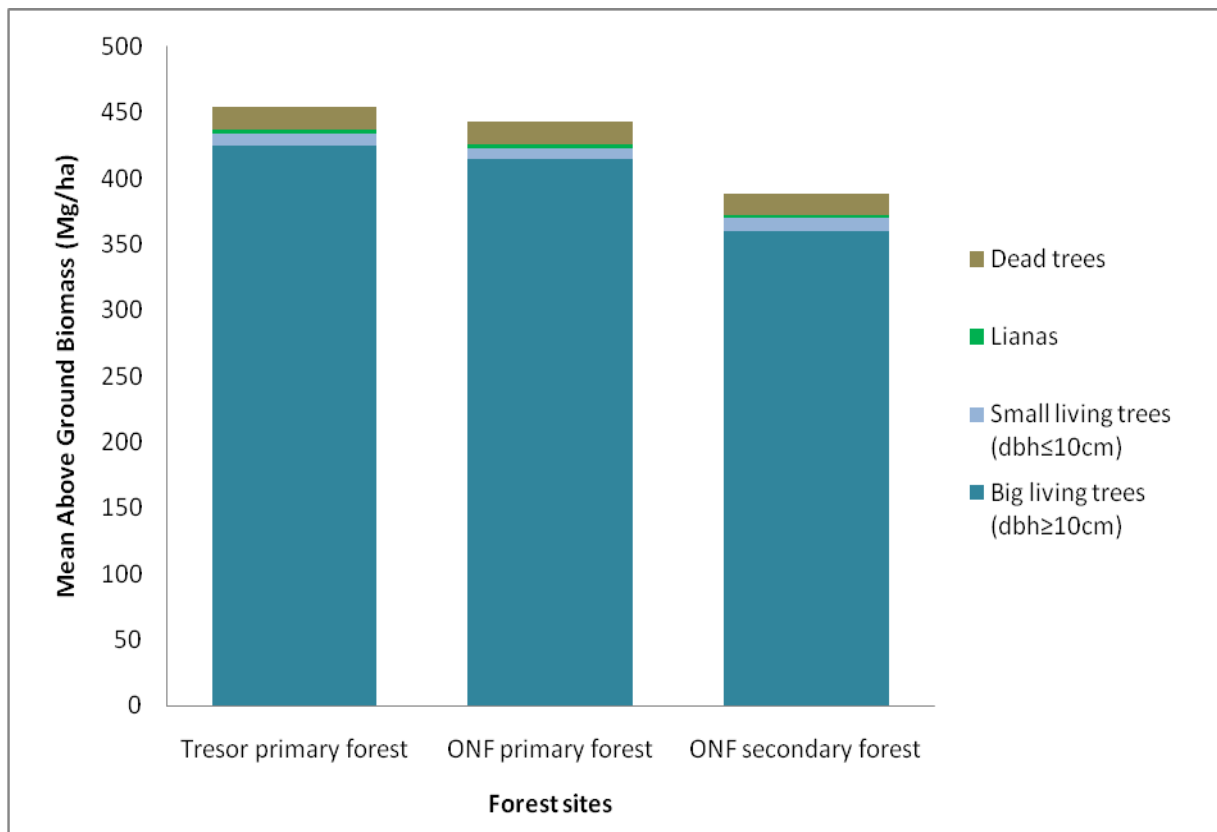


Figure 5. Mean AGB (in Mg/ha, $n=3$) in the three forest sites in the Kaw Mountains: primary forest in the Trésor nature reserve, primary forest in the ONF area and secondary forest in the ONF area. AGB is separated into four different categories: dead trees (in brown), lianas (in green), small living trees of DBH between 2.5 cm and 10 cm (in light blue), and big living trees of DBH of 10 cm and more (in dark blue).

Table 4. Table of all the categories of mean AGB values (Mg/ha, n=3) calculated for the three different forest sites studied: primary forest of the Trésor nature reserve, primary forest of ONF and secondary forest of ONF. In addition, the standard error of the mean was calculated for all mean AGB estimates. For each category, differences in AGB between the three forest sites were tested statistically using ANOVA analysis. The p-values obtained from the ANOVA tests are shown in the table.

AGB categories	Trésor Primary forest (\pm SE)	ONF Primary forest (\pm SE)	ONF Secondary forest (\pm SE)	Significance (p-value)
AGB of big living trees (DBH \geq 10cm)	424.41 \pm 52.13	414.46 \pm 11.51	360.18 \pm 33.09	0.4521
AGB of small living trees (DBH \leq 10cm)	9.56 \pm 0.38	7.95 \pm 4.30	9.87 \pm 1.65	0.8651
AGB of dead trees	16.71 \pm 4.28	17.28 \pm 6.08	16.24 \pm 3.71	0.9882
AGB of lianas	3.13 \pm 2.81	3.34 \pm 2.50	1.77 \pm 0.06	0.8604
Total AGB	453.81 \pm 45.46	443.03 \pm 8.81	388.06 \pm 38.00	0.4095

Figure 5 and Table 4 show that as expected the total AGB in the logged forest of ONF is lower (388.06 Mg/ha) than in both the primary forests of Trésor reserve and ONF area. Furthermore, there is a slight difference in total AGB between the two primary forests, with the primary forest of the Trésor nature reserve having a higher total AGB (453.81 Mg/ha) than that of the ONF area (443.03 Mg/ha). These observed differences in total AGB between the three forest sites are mainly due to the AGB of big living trees (DBH \geq 10cm). From Figure 5 and Table 4, it is evident that the AGB of big trees constitutes most of the total AGB in each forest site. The additional information provided by Appendix 4 shows that the big living trees comprises on average 93.3% of the total AGB when combining all three forest sites. In comparison, the average contribution in respective order of dead trees (3.9%), small living trees (DBH \leq 10cm; 2.1%) and lianas (0.6%) to the total AGB is very low for all three forest sites (Appendix 4). Thus, the low total AGB in the secondary forest of ONF is primarily explained by its low AGB of big living trees (360.18 Mg/ha). In addition, the AGB of big living trees in the primary forest of ONF is relatively lower (414.46 Mg/ha) than in the primary forest of Trésor (424.41 Mg/ha) which mainly explains the differences observed in total AGB between these two primary forest sites. Since the differences in total AGB between the three forest sites in the Kaw Mountains are mainly due to differences in the AGB of big living trees, a boxplot was produced to provide further information on this variable for data interpretation (Figure 6).

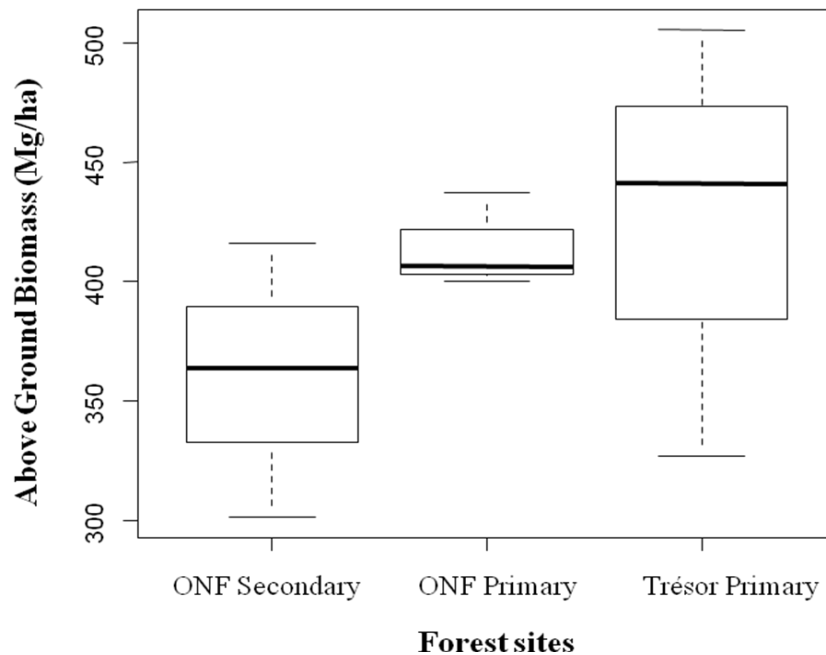


Figure 6. Boxplot showing the variation in AGB (Mg/ha) of the big living trees (DBH \geq 10cm) between the three different forest sites in the Kaw Mountains.

The boxplot in Figure 6 shows the spread of the variation in AGB of big living trees (DBH \geq 10cm) for each forest site. From the histogram in Figure 5 and Table 4, it was earlier underlined that the mean AGB of big living trees in the primary forest of ONF is slightly lower than in the primary forest of Trésor. Nevertheless, Figure 6 shows that the overall variation in the AGB of big living trees is very large in the Trésor nature reserve in comparison to that of the ONF primary forest. In the Trésor nature reserve, the AGB of big living trees varies from a maximum value of 505.43 Mg/ha to a minimum value of 327.07 Mg/ha. This large range in AGB values explains the high standard error of the mean AGB of big living trees in the Trésor forest of 52.13 Mg/ha (see Table 4). On the other hand in the primary forest of ONF, the range of the AGB of big living trees is much smaller with a maximum value of 437.20 Mg/ha and a minimum of 400.06 Mg/ha, resulting in a lower standard error of the mean AGB of 11.51 Mg/ha (see Table 4).

Furthermore, the variation in the AGB of big living trees in the logged forest of ONF is also relatively high since it varies between 301.37 Mg/ha and 415.86 Mg/ha, resulting in a mean standard error of 33.09 Mg/ha (see Table 4). Thus there is an overlap between the logged ONF forest and both of the primary forests in the range of the variation in AGB of big living trees. However it should be taken into consideration that only one stump had been recorded inside the Gentry plot in the logged forest which contained the highest value of big living trees AGB (415.86 Mg/ha). Meanwhile the other two Gentry plots had at least two or three stumps found inside the sampled area. This suggests that the logging intensity may have been lower in the area of that specific Gentry plot which could in turn explain the relatively high values obtained in the AGB of big living trees.

Finally, the differences in AGB between the three different forest sites were investigated statistically using ANOVA. Table 4 presents the p-values obtained from the ANOVA test among the different AGB categories. The high p-values suggest that there are no significant differences between the three forest sites for all the categories of AGB.

3.2. Selective logging effect and local spatial variation in forest structure in the Kaw Mountains

Two features of the forest structure, stem density (number of trees/hectare) and basal area ($\text{m}^2/\text{hectare}$) were analyzed. The ANOVA analysis showed that for these two features there are no significant differences between the three different forest sites in the Kaw Mountain (Table 5). Despite the fact that there are no significant differences, it can be observed that the logged forest of ONF contains the highest total amount of trees per hectare (2348 trees/ha) but the smallest total basal area ($31.3 \text{ m}^2/\text{ha}$). This could be explained by the distribution of trees in the different DBH categories, which is shown in Table 6, page 34. The secondary forest of ONF contains a higher number of trees of very small DBH size (2.5-5 cm) and a lower number of trees of very large DBH size ($\geq 70 \text{ cm}$) in comparison to the two primary forest sites. Furthermore, the primary ONF forest contains higher stem density and basal area than the primary forest in the Trésor nature reserve. Table 6 shows that the primary ONF forest contains overall a higher number of trees per hectare in both the smallest and largest DBH size classes (2.5-5 cm; 40-70 cm; $\geq 70 \text{ cm}$).

Finally, the general pattern for all three forest sites that can be observed from Table 6 is that the smallest DBH class (2.5-5 cm) contains the highest amount of trees and the number of trees distributed in bigger DBH size classes decreases gradually.

Table 5. Stem density (number of trees/ha) and basal area (m^2/ha) for the three forest sites in the Kaw Mountains. The p-value obtained from the ANOVA analysis ($n=3$) between the different forest sites is included.

Forest structure	Trésor Primary forest ($\pm\text{SE}$)	ONF Primary forest ($\pm\text{SE}$)	ONF Secondary forest ($\pm\text{SE}$)	Significance (p-value)
Stem density (#/ha)	1876 \pm 86.19	2210 \pm 397.00	2348 \pm 270.16	0.5
Basal area (m^2/ha)	33.5 \pm 3.94	37.3 \pm 1.58	31.3 \pm 1.79	0.3

Although no significant difference was found between the total stem density of the three forest sites, on the other hand the Pearson's Chi-square test indicated that there are significant differences between the distribution of trees within the different DBH classes (p-value 0.00).

To determine which specific DBH classes for each forest site had a major influence on the significant Pearson's Chi-square test result, the standardized residuals obtained from the Chi-square test were examined. The table showing these residuals is included in Appendix 5. When the absolute value of the standardized residual is greater than 2, it is considered to be significantly large to be able to conclude that the Observed Frequency count in the cell in question is significantly different from that which would have been expected had there been no association between the two variables. The number of trees per hectare belonging to the DBH class for which the absolute value of the standardized residual was greater than 2 are represented in bold in Table 6. Thus, the large number of trees per hectare in the very small DBH size class (2.5-5 cm) for the secondary ONF forest had a major contribution to the Chi-square test results. Additionally, the number of trees per hectare in the 10-20 cm DBH classes for both the primary forest and secondary forest of ONF had a major influence on the Chi-square test results. Finally, the number of trees per hectare in the 20-30 cm DBH class for both the primary forest of Trésor and the secondary forest of ONF made also a major contribution to the Chi-square test results.

Table 6. Distribution of trees (number of trees per hectare and associated percentages) within the different DBH classes for each of the three different forest sites in the Kaw Mountains. The number of trees per hectare are in bold when the absolute value of its standardized residuals obtained from the Pearson's Chi-square test was greater than 2, which means that it had a major influence on the significant Chi-square test.

DBH classes	Trésor Primary		ONF Primary		ONF Secondary	
	Number trees per ha	Percentage (%)	Number trees per ha	Percentage (%)	Number trees per ha	Percentage (%)
2.5 to 5 cm	917	48.9	1085	49.1	1333	56.8
5 to 10 cm	517	27.5	570	25.8	563	24.0
10 to 20 cm	225	12.0	343	15.5	270	11.5
20 to 30 cm	107	5.7	97	4.4	77	3.3
30 to 40 cm	49	2.6	43	1.9	43	1.8
40 to 70 cm	47	2.5	54	2.4	51	2.2
70 cm and more	15	0.8	18	0.8	10	0.4
Total	1876	100.0	2210	100.0	2348	100.0

In conclusion, the Chi-square test showed that there are significant differences between the three forest sites in the number of trees per hectare, particularly within the DBH classes between 2.5 cm and 30 cm. Furthermore, in general a higher number of trees are found in the smaller DBH categories. Figure 7 shows the distribution within the different DBH classes of the percentage of number of trees per hectare and the percentage of the AGB per hectare for each forest site. From Figure 7, it becomes clear that the majority of the AGB lies within the largest DBH classes (40-70 cm and ≥ 70 cm) for all three forest sites. Moreover, the table in Appendix 6 gives the mean AGB values (Mg/ha) and associated percentages within the different DBH classes, which were used to construct the histograms in Figure 7. From Figure 7 and Appendix 6, the combined percentages of the AGB lying within the two largest DBH classes (40-70 cm and ≥ 70 cm) in Trésor primary forest, ONF primary forest and ONF secondary forest are 70.4%, 69.2% and 71.2%, respectively. Consequently, the most important component of the AGB are the large trees with a DBH equal or greater than 40 cm, which compromises on average about 70% of the total AGB in the three forest sites. In contrast, the contribution of very small trees ($2.5 \leq \text{DBH} \leq 5 \text{ cm}$) to the total AGB remains extremely small: 0.5% in Trésor primary forest, 0.6% in ONF primary forest and 0.7% in ONF secondary forest (see Appendix 6).

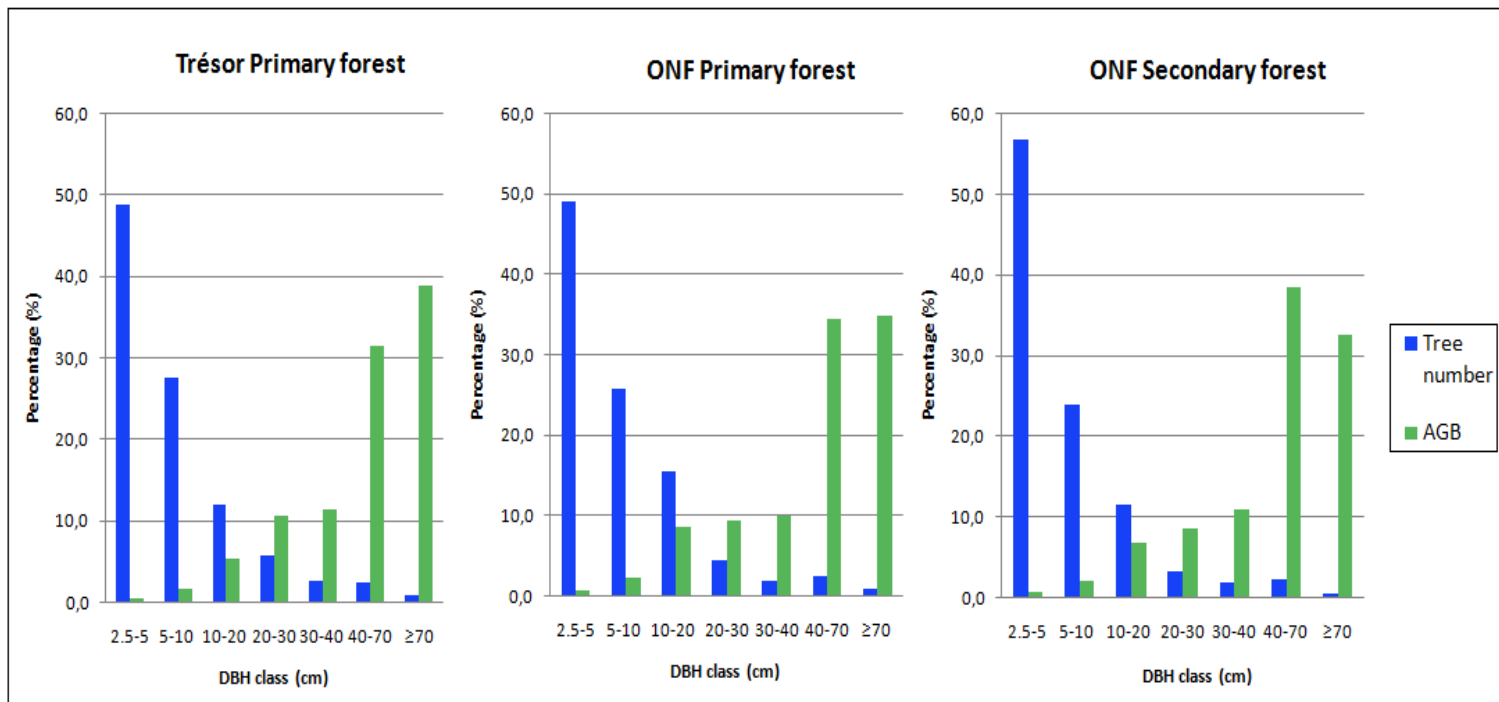


Figure 7. A histogram for each forest site showing the distribution within the different DBH classes (in cm) of the percentage of number of trees per hectare (in blue) and the percentage of the above-ground biomass (Mg) per hectare (in green).

3.3. Temporal variation in AGB due to selective logging activity in the Turtle Mountain and the Kaw Mountains

To clearly represent the changes over time in AGB caused by logging activity over the year 2005 in the Turtle Mountain, regression lines were fitted into the scatter plot graph in Figure 8. Firstly, the regression line in green represents the variation in AGB of big living trees (DBH \geq 10cm) in the control plot which remained protected from logging activity. The value of the slope of the regression line between 2002 and 2007 is of 1.16, which suggests that the AGB is gradually increasing over time when undisturbed at a rate of about 1.16 Mg/ha/yr.

Secondly, the red regression line in Figure 8 shows the sudden decrease in AGB of big living trees (DBH \geq 10cm) from before logging (in 2002) to two years after logging occurred (in 2007). More precisely, during this time period the AGB decreased from an average AGB of 454.42 Mg/ha to 367.31 Mg/ha (Table 7). Moreover, the value of the slope of the regression line between 2002 and 2007 is of -17.421. On the other hand, the slope of the regression line between 2007 and 2010 (in blue) has a positive value of 0.2217 which suggests that there is a relative increase in AGB after logging activity at a rate of about 0.22 Mg/ha/yr. However, when comparing the values of the average AGB between 2007 and 2010, it becomes clear that this increase in AGB is very small. The average AGB increased from 367.31 Mg/ha to 367.98 Mg/ha between 2007 and 2010 (Table 7). Furthermore, it should also be taken into consideration that the patterns of change in AGB between 2007 and 2010 of the two distinct logged plots are completely different. In Appendix 3, the exact AGB values for each logged plot can be found. For logged plot A, the AGB increased from 381.31 Mg/ha in 2007 to 390.26 Mg/ha in 2010, representing an AGB gain of 2.98 Mg/ha/yr. Whereas for logged plot B, the AGB decreased from 353.31 Mg/ha in 2007 to 345.69 Mg/ha in 2010, representing an AGB loss of 2.54 Mg/ha/yr. As a result, despite the overall increase in mean AGB from 2007 to 2010, there are actually conflicting patterns of changes in AGB between the two distinct logged plots in the Turtle Mountain.

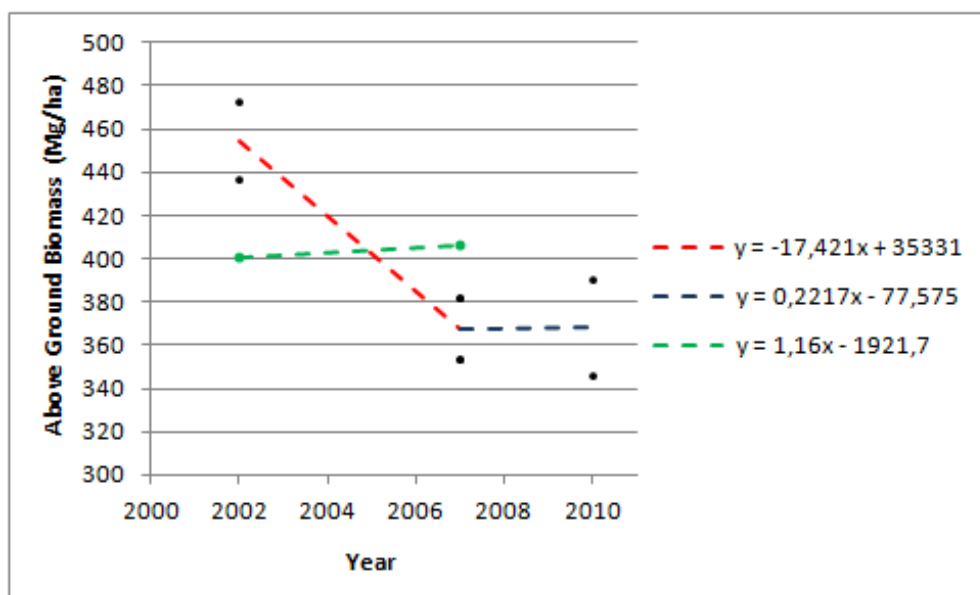


Figure 8. Graph showing the changes in the above-ground biomass (Mg/ha) over time in two plots in the Turtle Mountain where logging occurred in 2005 (regression lines represented in red for 2002-2007 and in blue for 2007-2010). The equations obtained from the segmented linear regression analysis are shown in the legend. In addition, the changes from 2002 to 2007 in the above-ground biomass (Mg/ha) of the control plot (where no logging occurred) in the Turtle Mountain is represented by the green regression line.

Despite the observed variation in AGB in the logged plots over time in Figure 8, the results of the ANOVA analysis (Table 7) reveal that there is no significant difference between the mean AGB in 2002, 2007 and 2010 (p-value 0.06765). Furthermore, the results of the segmented regression analysis (Table 8) for the AGB from the logged plots show that the difference between the regression lines for 2002-2007 and 2007-2010 is non-significant (p-value 0.0603 and 0.982 respectively). The non-significant results for both these statistical analyses could partly be explained by the low amount of replicates (only two replicates for the logged plots).

Table 7. Table showing the mean AGB (Mg/ha, n=2) of the logged plots in the Turtle Mountain for 2002, 2007 and 2010. The p-value obtained from the ANOVA analysis on the three mean AGBs is included.

Turtle Mountain	2002 (\pm SE)	2007 (\pm SE)	2010 (\pm SE)	Significance (p-value)
Mean AGB (Mg/ha)	454.42 \pm 17.52	367.31 \pm 14	367.98 \pm 22.29	0.06765

Table 8. Table presenting the results of the segmented regression analysis (n=2) for 2002-2007 and 2007-2010.

Years	Regression Coefficient	Standard Error	T-value	Significance (p-value)
2002 - 2007	-17.421	4.485	-3.885	0.0603
2007 - 2010	0.2217	8.7726	0.025	0.982

The boxplot in Figure 9 was produced to compare the AGB estimates (of big trees with $DBH \geq 10\text{cm}$) obtained 5 years after selective logging in both the Turtle and Kaw Mountains. Figure 9 shows that in general the AGB data from both forest sites are very similar because their boxplots contain approximately the same values for upper quartile and median. Furthermore, there appears to be more variation in AGB in the Kaw Mountains since the boxplot for the Kaw Mountains contains whiskers whereas the boxplot for the Turtle Mountain does not contain any. This can be explained by the fact that the AGB estimates in the Turtle Mountain lie within the boundaries of the boxplot which is not the case for the AGB estimates in the Kaw Mountains. To conclude, a t-test was carried out on the AGB data which showed that there is no significant difference between the mean AGB of the two secondary forests in Kaw and Turtle Mountains (p-value 0.8758).

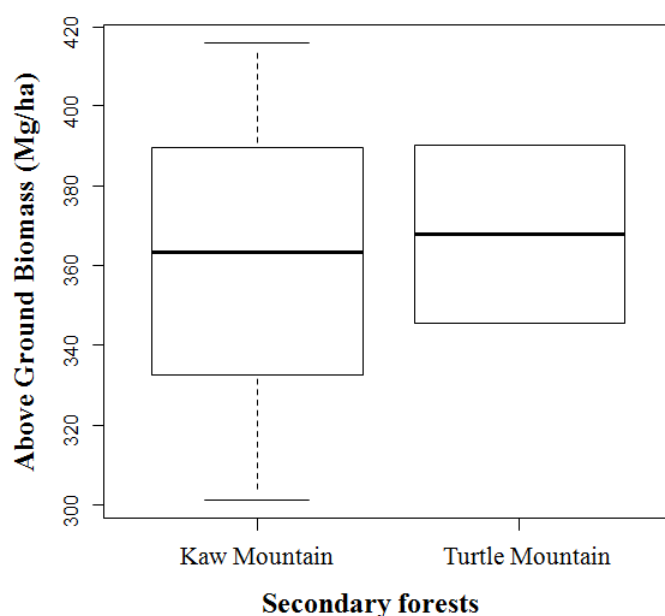


Figure 9. Boxplot of the above-ground biomass (Mg/ha) in the secondary forests in the Kaw Mountains (n=3) and Turtle Mountain (n=2).

Finally, the predicted temporal variation in AGB over the next 50 years for both the primary and secondary forests in the Kaw Mountains and Turtle Mountain are presented in Table 9, page 38. As explained in the methods, the rate of AGB accumulation used for the primary forest (1.4 Mg/ha/yr) and secondary forest (2.6 Mg/ha/yr) was based on the study by Mazzei et al. (2010). Table 9 shows that the mean AGB in the secondary forest in the Kaw Mountains is expected to increase from 360.18 Mg/ha in 2011 to 490.18 Mg/ha in 2061. Meanwhile, the mean AGB in the primary forest in the Kaw Mountains is expected to increase from 419.43 Mg/ha in 2011 to 489.43 Mg/ha in 2061. Moreover for the Kaw Mountains, the mean AGB in its secondary forest is expected to reach a similar value to the mean AGB in its primary forest in 2011 (419.43 Mg/ha) after 2031.

Table 9 shows that the mean AGB in the primary and secondary forests in the Turtle Mountain is expected to increase from 410.60 Mg/ha and 367.98 Mg/ha in 2010 to 480.60 Mg/ha and 497.98 Mg/ha in 2060, respectively. Furthermore, the mean AGB in the secondary forest in the Turtle Mountain before logging occurred was 454.42 Mg/ha in 2002 (see Table 7). From table 9, the mean AGB in the secondary forest is expected to increase to 458.98 Mg/ha in 2045. In consequence, according to these predictions the AGB in the secondary forest in the Turtle Mountain is expected to recover by 2045 from the detrimental effects of the logging activity in 2005. In other words, the recovery of the AGB from selective logging in the Turtle Mountain is

expected to take about 35 years. No similar conclusions can be made for the Kaw Mountains due to the lack of information about AGB values before logging activity occurred.

Table 9. The rate of AGB accumulation (Mg/ha/yr) and the changes in AGB (Mg/ha) over the years for both the Turtle Mountain and the Kaw Mountains.

Turtle Mountain	rate of AGB accumulation (Mg/ha/yr)	Changes in mean AGB over the years (Mg/ha)							
		2007	2010	2020	2030	2040	2045	2050	2060
Primary forest	1.4	406.40	410.60	424.60	438.60	452.60	459.60	466.60	480.60
Secondary forest	2.6	367.31	367.98	393.98	419.98	445.98	458.98	471.98	497.98

Kaw Mountain	rate of AGB accumulation (Mg/ha/yr)	Changes in mean AGB over the years (Mg/ha)					
		2011	2021	2031	2041	2051	2061
Primary forest	1.4	419.43	433.43	447.43	461.43	475.43	489.43
Secondary forest	2.6	360.18	386.18	412.18	438.18	464.18	490.18

3.4. Comparison of the mean AGB between primary forest sites in French Guiana

In Figure 10, the boxplot gives an overview of the variation in the AGB across five different primary forest sites in French Guiana. This boxplot shows that in general the ranges of variation in AGB of the different forest sites do overlap. The primary forest in Trinité contains the highest AGB values but also the greatest amount of variation in AGB which can be deduced from the length of its box and whisker plot. In Trinité, the lowest AGB estimate is of 244.28 Mg/ha whilst the highest AGB estimate reaches 604.87 Mg/ha. These conclusions are confirmed when also examining the mean AGB values given in Table 10. The Trinité forest has the highest mean AGB of 465.43 Mg/ha but also the highest standard error of the mean of 52.85 Mg/ha.

After the Trinité forest, the primary forest in the Kaw Mountains contains the highest mean AGB of 419.43 Mg/ha and on the other hand a relatively low standard error of the mean AGB, 23.98 Mg/ha (Table 10). Furthermore, Figure 10 also suggests that there is relatively low variation in the AGB in the Kaw Mountains because its boxplot is of small size and its upper and lower quartiles vary close to about 410 Mg/ha. However, the absence of whiskers in the boxplot of the Kaw Mountains is due to two outliers, which are represented instead by two dots in Figure 10.

The primary forest in Laussat contains the third highest mean AGB, 401.70 Mg/ha, and the lowest standard error of the mean, 22.58 Mg/ha (Table 10). When examining the boxplot of Laussat, the size of its boxplot is larger than that of the Kaw Mountains however it does not contain any outliers unlike for the Kaw Mountains, which is the reason for its lower standard error of the mean.

In fourth position is the forest in Regina with a mean AGB of 392.57 Mg/ha and a standard error of the mean AGB of 38.14 Mg/ha (Table 10). Finally, the primary forest in Nouragues has the lowest mean AGB, 366.29 Mg/ha, and a relatively high standard error of the mean, 43.82 Mg/ha (Table 10). In Figure 10, the boxplot of the Nouragues has the lowest 3rd quartile and lowest reaching whiskers in comparison to all the other forest sites. More precisely, the lowest AGB estimate in the Nouragues forest is 208.12 Mg/ha.

Despite all these variation in AGB between the different forest sites as described above, the ANOVA analysis (Table 10) showed that there is no significant difference between the mean AGB of the five forest sites (p-value 0.4546). This result suggests that there is no significant regional spatial variation in AGB between these geographically different forest sites.

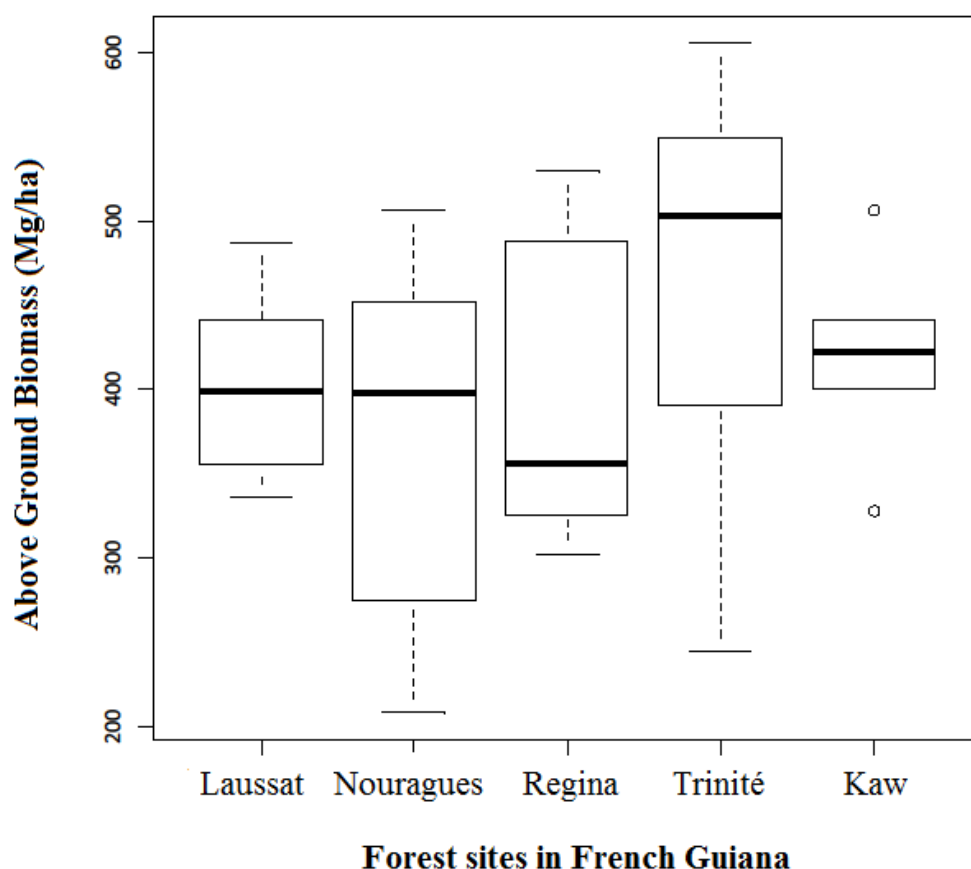


Figure 10. Boxplots showing the variation in the above-ground biomass (Mg/ha) in five different primary forest sites across French Guiana: Laussat (n=7), Nouragues (n=7), Regina (n=6), Trinité (n=6) and Kaw (n=6).

Table 10. The mean above-ground biomass (Mg/ha) in five different primary forest sites across French Guiana. The p-value obtained from the ANOVA analysis is included in the table.

Forest sites	Laussat (\pm SE)	Nouragues (\pm SE)	Regina (\pm SE)	Trinité (\pm SE)	Kaw (\pm SE)	Significance (p-value)
Mean AGB (Mg/ha)	401.70 \pm 22.58	366.29 \pm 43.82	392.57 \pm 38.14	465.43 \pm 52.85	419.43 \pm 23.98	0.4546

3.5. Multivariate analysis: regional spatial variation in AGB across French Guiana

A Principal Component Analysis (PCA) was carried out to study in further detail the potential regional spatial variation in AGB across French Guiana by examining the relationship between climate and stand variables with AGB. In order to achieve this, the PCA identifies which combinations of variables (AGB, climate and stand) explain the largest amount of variation in the dataset. These new combinations of variables generated by the PCA are referred to as principal components. Thus, the first principal component is chosen in order to explain the largest amount of information in the dataset. The second principal component is designed in such a way to be as

different as possible from the first meanwhile explain the second largest amount of information. Finally, the next principal components are constructed following this model.

The outcomes for the first three principal components from the PCA are given in Table 11. Principal Components One, Two and Three explain 36.58%, 21.45% and 13.76% of the variance in the dataset, respectively. Consequently, the first three principal components have captured 71.79% of the total information.

Table 11. Table showing the outcome of the PCA for the three first principal components: the percentage explained by each principal components towards the variation in the dataset and the component loadings of each individual variable for each principal component. The component loadings greater than 0.5 are represented in bold.

Principal Components		1	2	3
Percentage (%)		36.58	21.45	13.76
Cumulative Percentage (%)		36.58	58.03	71.79
Group	Individual variables	Component Loadings		
AGB variables	AGB (DBH \geq 10cm)	0.938	0.194	0.178
	Total AGB	0.937	0.177	0.165
	AGB (10cm \geq DBH \geq 2.5cm)	-0.127	0.830	0.226
Stand variables	Stems (DBH \geq 30cm)	0.846	0.274	-0.098
	Basal Area	0.817	0.341	-0.154
	DBH	0.625	-0.651	-0.034
	Height	0.713	-0.404	0.020
	Wood density	0.497	-0.254	0.193
	Stems (10cm \geq DBH \geq 2.5cm)	0.109	0.901	0.046
	Stems (30cm \geq DBH \geq 10cm)	-0.153	0.350	-0.396
Climate variables	DSI	0.082	-0.159	-0.800
	Rainfall	-0.211	0.350	0.818

Figure 11 and the component loadings given in Table 11 provide useful information in order to determine which combinations of variables are being represented by Principal Component One (PC1), Principal Component Two (PC2) and Principal Component Three (PC3). In Figure 11, the contribution of a variable to PC1 versus PC2 can be interpreted from its distance to and projection onto PC1 (on the x-axis) and PC2 (on the y-axis) which depends on the position, direction and length of its arrow.

Therefore, Figure 11 shows that PC1 has strong positive contributions from the total AGB and AGB of stems with DBH \geq 10 cm, followed closely by stem density of trees with DBH \geq 30 cm and finally basal area. Furthermore, this interpretation from Figure 11 is confirmed by the high and positive values of the component loadings of these four individual variables given in Table 11. Additionally, the Height and DBH variables also have high and positive component loadings for PC1 of 0.713 and 0.625 respectively (Table 11). In contrast, all the other remaining AGB, stand and climate variables do not contribute to a great extent to the value of the PC1 as shown in Figure 11 and by their low component loadings (below 0.5) presented in Table 11. Moreover, Appendix 7 provides further information about the relationship between stand variables and total AGB. Appendix 7 shows an overall positive correlation of total AGB with DBH and height and to an even stronger extent with large stem density (DBH \geq 30 cm) and basal area. However, there is a weak correlation between total AGB and wood density. In conclusion, PC1 represents a

gradient of increasing total AGB and AGB of big trees ($DBH \geq 10cm$) positively correlated with increasing DBH, height, large stem density ($DBH \geq 30cm$) and stand basal area.

As shown in Figure 11, the two main variables with the strongest positive contribution towards the second Principal Component are the AGB and stem density of small trees ($10cm \geq DBH \geq 2.5cm$). These results are also reflected by the values of their component loading given in Table 11. The component loading of the AGB and stem density of small trees are 0.830 and 0.901, respectively. Therefore, PC2 mainly represents a gradient of increasing AGB and stand variables of small trees ($10cm \geq DBH \geq 2.5cm$).

Figure 11 and Table 11 show that the two climate variables (DSI and rainfall) have little effect on the values of both PC1 and PC2. However, PC3 has strong opposing contributions of these two climate variables as suggested by the high positive component loading of rainfall (0.818) versus the high negative component loading of DSI (-0.800) given in Table 11. Furthermore in Appendix 8, the graph illustrating the contribution of the different variables towards constructing PC3 against PC4 was included for visual representation. The main conclusion is that PC3 is a contrast between the climate variable associated with rainfall and the climate variable associated with dryness (DSI), which explains only 13.76% of the variance in the dataset.

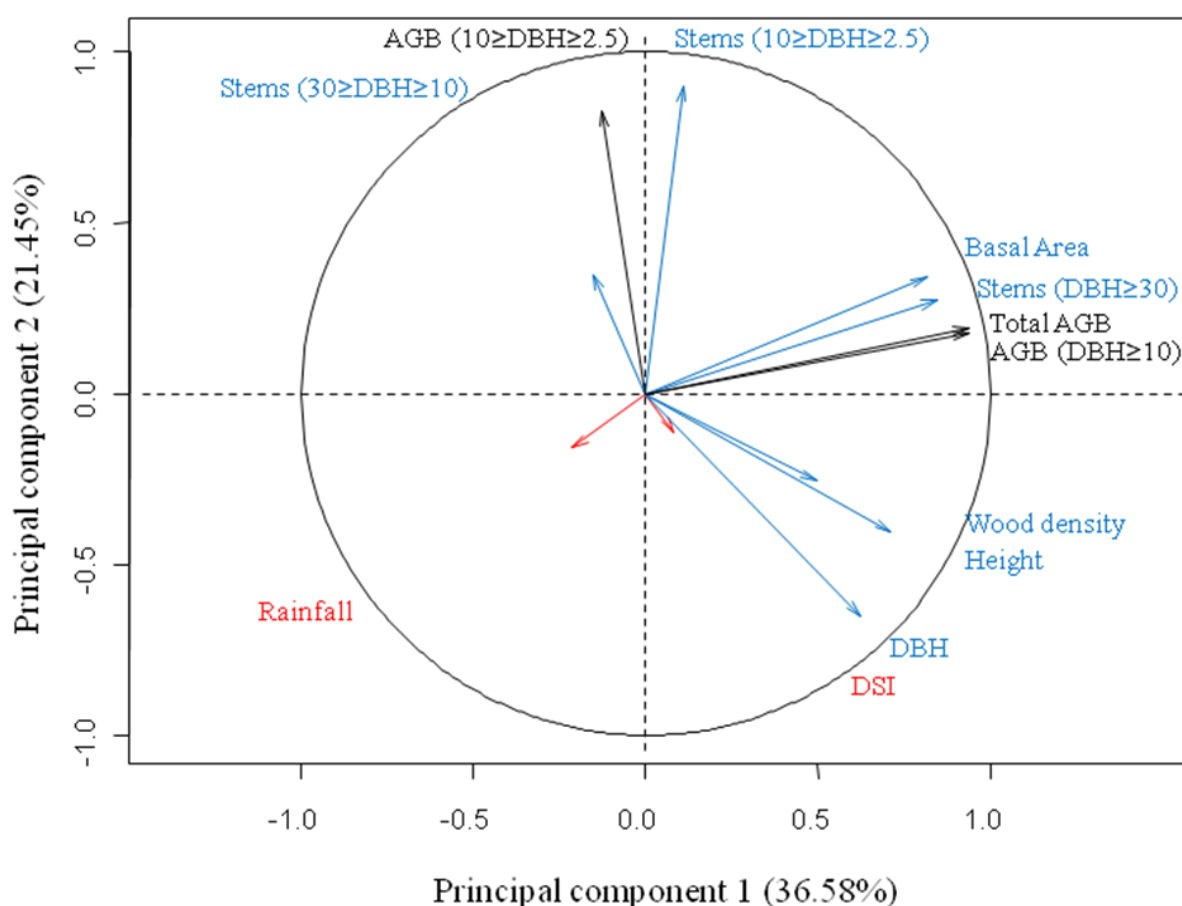


Figure 11. Graph representing the contribution of the twelve individual variables towards constructing Principal Component 1 on the x-axis (explaining 36.58% of the variance in the dataset) against Principal Component 2 on the y-axis (explaining 21.45% of the variance in the dataset). The stand, climate and AGB variables are illustrated respectively in blue, red and black.

After discussing which combinations of variables are being represented by the principal components, the next step is to analyse the scattergram generated by the PCA presented in Figure 12. This scattergram plots PC1 against PC2 because jointly they explain 58.03% of the variance in the dataset. The PC3 was not included into this analysis as it only explains 13.76% of the variance in the dataset. Furthermore, this scattergram plots the values of these newly constructed principal components for each of the different Gentry plots in our dataset (represented by circles in the graph). To be able to differentiate between the different forest sites, different plotting colours were used.

The scattergram in Figure 12 shows that the plotted data, representing each individual Gentry plot within the different forest sites (graphically represented by full coloured circles), are more or less evenly spread out across the graph. For clearer visual representation, the coordinates of all the plotted data for each forest site were gathered to provide a general result for each forest site (graphically represented by empty coloured squares). Therefore, from this scattergram there appears to be no clear trend separating the different forest sites because the general results obtained for each forest site are all clustered towards the center of the graph. Despite the fact that AGB and stand variables strongly contributed to the construction of PC1 and PC2, no clear trend of geographical separation by AGB and stand factors can be detected from the scattergram. These results demonstrate that there are no spatial patterns in AGB between these different forest sites in French Guiana. However, Trinité does stand out slightly from the other forest sites in the scattergram in Figure 12. The position of the Trinité data in the graph suggests that in comparison to the other forest sites, the Trinité forest contains both high total AGB, stem density of large trees ($DBH \geq 30\text{cm}$) and basal area while at the same time high AGB and stem density of small trees ($10\text{cm} \leq DBH < 30\text{cm}$). These findings explain the very high variation in AGB within the Trinité forest observed earlier from the boxplot in Figure 10. Furthermore, the position of the Nouragues data on the graph also suggests that Nouragues has relatively lower total AGB, stem density of large trees ($DBH \geq 30\text{cm}$) as well as lower basal area in comparison to the other forest sites. These findings also reinforce the previous observations made from the boxplot in Figure 10, which showed that Nouragues contained overall the lowest values of AGB.

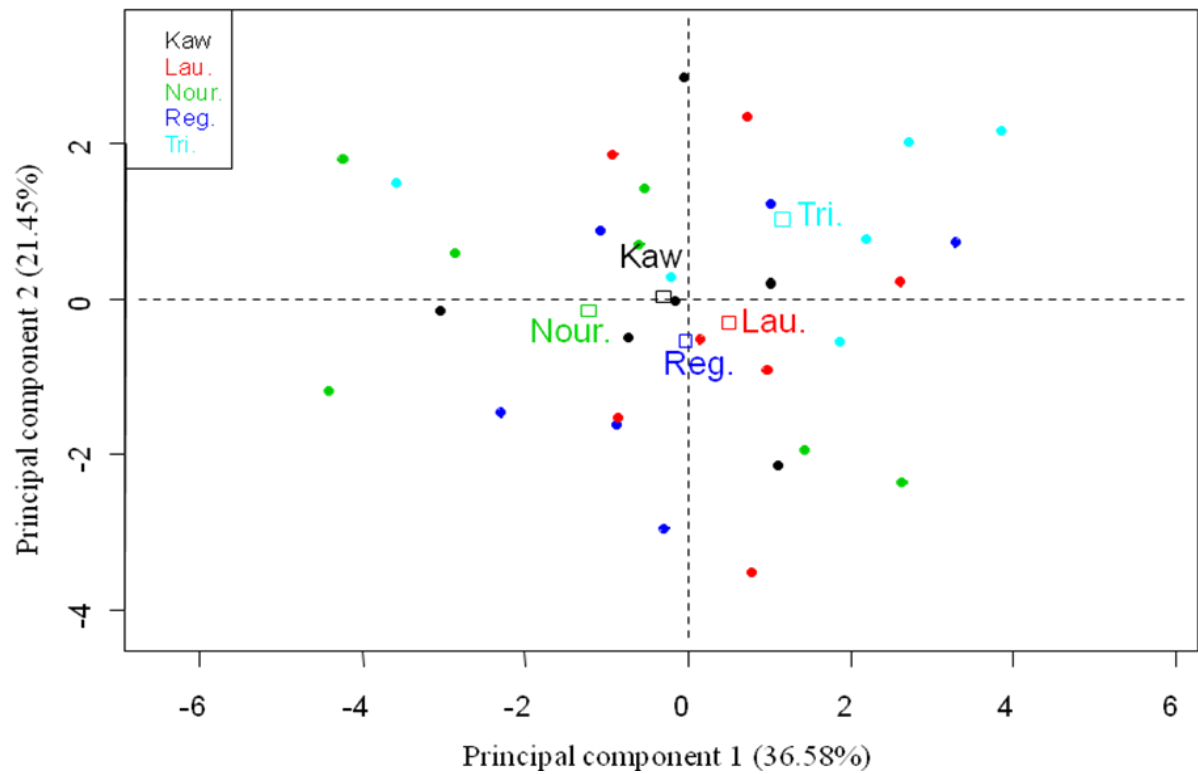


Figure 12. Scattergram of the values obtained from the Principal Component Analysis (PCA) when plotting Principal component 1 on the x-axis (explaining 36.58% of the variance in the dataset) against Principal component 2 on the y-axis (explaining 21.45% of the variance in the dataset) for five different forest sites in French Guiana: Kaw (in black), Laussat (in red), Nouragues (in green), Regina (in dark blue) and Trinité (in light blue).

4. Discussion

4.1. The contribution of lianas, dead trees, small living trees (DBH≤10cm) and big living trees (DBH≥10cm) to the total AGB estimates in the Kaw Mountains

The total AGB estimates in the Kaw Mountains varied among the three forest sites from 388.06 to 453.81 Mg/ha (Figure 5 and Table 4). These values are comparable to those reported in other forest sites in French Guiana. For example, the study by Rutishauser et al. (2010) in Paracou found that AGB estimates varied among plots from 388 to 443 Mg/ha. However, these values are higher than the Amazonian average of 288.6 Mg/ha (value based on 227 plots from 105 locations taken from Malhi et al., 2006).

The AGB of big living trees (DBH≥10cm) was found to constitute most of the total AGB in the three forest sites in the Kaw Mountains (primary Trésor, primary ONF and secondary ONF). Moreover, it comprised on average 93.3% of the total AGB when combining the results of all three forest sites (Appendix 4). In addition, when investigating the distribution of the AGB in the different DBH classes (Figure 7 and Appendix 6) it became evident that the most important component of the AGB was the large trees with a DBH of 40 cm or more, which made up a disproportionately large part (about 70%) of the total AGB despite their low numbers. Several studies also emphasize the crucial role of large trees to AGB estimates in tropical forests (Clark & Clark, 1996; Chave et al., 2004; DeWalt & Chave, 2004; Rutishauser et al., 2010). For an example, Brown and Iverson (1992) calculated that in a tropical forest the AGB of one large tree of 150cm in diameter equals that of approximately 607 small trees of 10cm in diameter.

In this study, the overall contribution of dead trees (3.9%), small living trees (2.1%) and lianas (0.6%) to the total AGB for all three forest sites was found to be very low, in respective order. The study by Nascimentoa and Laurance (2002) in an undisturbed Brazilian Terra Firme forest reported similar results. Their research showed that the AGB of big trees (DBH≥10cm) constituted 81.9% of the total AGB, followed by dead trees (7.0%), small trees (DBH≤10cm; 5.3%) and lianas (2.1%). Apart from this study by Nascimentoa and Laurance (2002), very few studies have attempted to quantify the contribution of dead trees, small trees and lianas to the total AGB in tropical forests. One obvious reason why most studies tend to ignore dead trees, lianas and small trees is due to the time required for adequate measurement. As a result, information about their potential contribution is relatively sparse. For example, estimates of the biomass of dead trees in tropical forests vary widely from 0 to over 60 Mg/ha (Baker et al., 2007; Clark et al., 2002; Rice et al., 2004).

Regardless of their exact contribution, it is recognized that dead trees, lianas and small trees do play a vital role in many aspects of forest dynamics such as forest regeneration, forest turnover rates, species diversity and ecosystem-level processes (Schnitzer & Bongers, 2002; Nascimentoa & Laurance, 2002; Liu et al., 2006; Schnitzer et al., 2006; Baker et al., 2007). Therefore, they are likely to have a significant effect to the forest carbon budget in the long-term by contributing in different ways to overall forest dynamics. In conclusion, despite their apparent low contribution to AGB, further studies should not systematically overlook them as over longer timescales they are likely to influence significantly the AGB as well as biodiversity patterns in tropical forests.

4.2. The effect of selective logging on the AGB and forest structure in the Kaw Mountains

The low mean AGB values of big living trees (DBH≥10cm) found in the secondary forest of ONF (360.18 Mg/ha) in comparison to both the primary forests of Trésor (424.41 Mg/ha) and ONF area (414.46 Mg/ha) suggest that the logging activity in 2006 did have a negative effect on the AGB (Figure 5 and Table 4). However, this difference in the AGB between primary and secondary forest sites was found to be non-significant as well as for the AGB of dead trees, lianas and small living trees.

An important factor which could explain these non-significant results is due to the low amount of Gentry plot replicates used for the data analysis ($n=3$). Furthermore, within the logged ONF forest the AGB of big living trees varied between 301.37 and 415.86 Mg/ha, resulting in a mean standard error of 33.09 Mg/ha (Table 4). This relatively high variation in AGB within a small amount of sampled plots increases the uncertainty of the results. In consequence, the non-significant results obtained when comparing the logged and unlogged plots in this study should be viewed with caution because of the low amount of replicates used, resulting in low statistical power.

Another important factor that should be taken into consideration when analysing the AGB results is linked to the potential variation in the logging intensity between the different plots. In general, the intensity of the disturbance caused by selective logging is related to the number of trees harvested and the amount of damage made by the logging equipment (Villela et al., 2006). Under selective logging, only a small number of specific trees are targeted (Asner et al., 2005). As a result, the effects of selective logging are not homogeneous over an entire forest area. To make sure that the Gentry plots in this study were set up in areas that had been recently exploited; the baseline was placed along the leftover tracks made by heavy forestry machinery. However, the number of stumps recorded in each Gentry plots (0.5 hectare) varied between one to three stumps. Moreover, the Gentry plot which contained the highest AGB value of big living trees (415.86 Mg/ha) was found to contain only one stump. These findings suggest that the logging intensity may have been lower within that specific Gentry plot, resulting in higher AGB estimates. Therefore, future studies investigating the effect of selective logging should aim to better control for logging intensity in order to improve the accuracy of their results. To do so, a suggestion would be to take the time to strategically count the exact number of stumps present within a 1 hectare area before setting up the Gentry plot.

Furthermore, logging activity appeared to have an impact on forest structure as the logged forest of ONF contained the highest total amount of trees per hectare (2348 trees/ha) but the smallest total basal area (31.3 m²/ha; Table 5), which is characteristic of secondary forests (Brown & Lugo, 1990). Moreover, these findings can be explained by the high number of trees of in the smallest DBH size (2.5- 5 cm) and the low number of trees of very large DBH size (70 cm and more) in the secondary forest (Table 6). Although total stem density and basal area were not significantly different between logged and unlogged forests, the distributions of trees within the different DBH classes were found to be significantly different. In particular, the high density of very small trees (DBH \leq 5cm) in the secondary forest contributed to this significant result. These findings can be linked to the fact that forest regeneration after recent logging activity, results in the establishment of a high number of small trees. As an example, the research carried out in Brazil by Magnusson et al. (1999) showed that the density of small trees (DBH \leq 10cm) was significantly greater in logged plots than in unlogged plots when measured 3 and 7 years after logging.

Several studies have shown that selective logging does not only alter the forest structure but also the composition of forest stand, reducing the number of shade tolerant species and stimulating light demanding species (Villela et al., 2006; Silva et al., 1995; Deckker & de Graaf, 2003; Okuda et al., 2003). Furthermore, Magnusson et al. (1999) found that species richness was significantly higher in the logged plots due to the overall increase in the number of small trees in the established regeneration. Initially, this research project had also planned to study species richness and diversity in the Kaw Mountains. Due to the incomplete field data on tree species, these biodiversity aspects could not be accurately analysed in this study. However, the team of botanists from CIRAD and EcoFoG are currently working on the identification of all the unknown tree species sampled. Therefore, this data will be useful for future studies wanting to study the impact of selective logging on biodiversity patterns in the Kaw Mountains. Furthermore, future research is needed to understand how different components of biodiversity influence AGB and carbon sequestration capacity in order to develop an effective REDD+ scheme.

4.3. Local spatial variation in AGB and forest structure in the Kaw Mountains

The mean AGB of big living trees (DBH \geq 10cm) in the primary forest of Trésor and ONF differed by only 9.95 Mg/ha, with the primary forest of the Trésor having a slightly higher AGB (424.41 Mg/ha) than that of the ONF area (414.46 Mg/ha; Table 4). Consequently, no significant difference was found between the mean AGB of these two primary forest sites. These results suggest that there is no difference in mean AGB between the two primary forest sites based on their spatial location in the Kaw Mountains. However, the relatively high range of variation in AGB within the Trésor forest only (327.07-505.43 Mg/ha) in comparison to the ONF forest (400.06-437.20 Mg/ha) raises concern about the accuracy of the results (Figure 6). Therefore, caution should be taken when interpreting these results since the variability in the dataset and the low number of Gentry plot replicates may have contributed to the non-significant outcome. In the meantime though, there appears to be no clear local spatial patterns in AGB between these two primary forest sites. Consequently, the AGB results from these two forest sites were combined in order to compare the mean AGB in the Kaw Mountains with other forest sites across a larger spatial-scale in French Guiana.

When studying the forest structure, no significant differences were found for both stem density and basal area between the two primary forest sites. On the other hand, their distribution of trees within the different DBH classes did significantly differ. The ONF forest had a significantly higher number of trees per hectare lying within the 10-20 cm DBH class whereas the Trésor forest had a significantly higher number of trees per hectare lying within the 20-30 cm DBH class (Table 6). The particular reason for this difference remains unclear. Further investigation would be needed to determine the potential factors causing this difference in forest structure, such as species composition or succession stage after natural or anthropogenic disturbances. Rutishauser et al. (2010) described tropical forests as a mosaic of patches at different stages of regeneration due to small-scale natural disturbances (i.e. tree falls). These patches are likely to be characterized by different DBH class structure, which could be an explanation for the differences found between these two forest sites in the Kaw Mountains.

For this study, a lot of care was taken to select sites of similar forest habitat (Terra Firme forest on flat hilltops) using expert knowledge, GIS map information and field surveys. However, several different forest types are present in the Kaw Mountains, among which seven forest types have been identified in the Trésor nature reserve (Ek et al., 2000). Therefore, to have a better estimation of the overall AGB stored in the Kaw Mountains, it would be necessary to compare the potential differences in AGB among the different forest types. For example, Kruijt et al. (2006) reported low AGB estimates in the Trésor savannas due to the fact that they consist mainly of grassland and low palms. In addition, the position of the forest in the Kaw Mountains is likely to have an influence on the AGB. A study by Ferry et al. (2010) in French Guiana found that the AGB dramatically decreased along a topographic gradient from hilltops to bottomlands, due to higher rates of tree fall which decreased the stand basal area and favored the recruitment of fast-growing species with low wood density. This large variation in AGB along the gradient underlines the importance of determining these characteristics when scaling up AGB estimates from stand to local or regional scales. Moreover, future research is needed to determine how the combination of different environmental factors may drive variation in AGB along this topographic gradient, such as the slope exposure to sun, wind or heavy rainfall.

4.4. Temporal variation in AGB due to selective logging activity

Logging activity in the Turtle Mountain in 2005 caused a major decrease in AGB from an average AGB of 454.42 Mg/ha in 2002 to an average AGB of 367.98 Mg/ha in 2010 (Table 7). Moreover, the AGB values in the secondary forests 5 years after logging in the Turtle Mountain and Kaw Mountains were found to be very similar (Figure 9). In general, the logging intensity in both

forest sites is comparable (about 4 to 6 stems/ha), except for maybe one Gentry plot in the Kaw Mountains where logging intensity may have been lower as discussed earlier. Therefore, it seems that both secondary forest sites showed a similar amount of damage on the AGB due to recent selective logging.

For the purpose of this study, the AGB in 2002 was considered as a reference for the AGB prior to harvesting in the Turtle Mountain. As a result, the logging activity in 2005 resulted in AGB losses from felled trees and collateral damage of 87.11 Mg/ha by 2007, which represents 19% of the estimated 454.42 Mg/ha prior to logging (Table 7). According to the study by Mazzei et al. (2010) in a Brazilian Terra Firme forest, the AGB is expected to still decrease during the first post-harvest years mainly due to the high mortality rate of trees damaged by logging. Therefore, it is likely that the AGB may have decreased during the two first years after logging (2005-2007) in the Turtle Mountain due to collateral damages. During the following three years (2007-2010), a low increase in mean AGB was detected at a rate of about 0.22 Mg/ha/yr. However, conflicting results were found since in one logged plot (plot A) the AGB was increasing by 2.98 Mg/ha/yr whereas in the other (plot B) the AGB was still gradually decreasing by 2.54 Mg/ha/yr (Appendix 3). Therefore, no clear overall pattern of changes in AGB could be determined for 2 to 5 years after logging in the Turtle Mountain because of opposite results obtained from only two replicates. Consequently, the low sample size represents a major limitation in this analysis. It is also worth noting that the lack of any significant difference between the regression lines and AGB estimates in 2002, 2007 and 2010 could be partly due to the low amount of replicates. Increasing the sample size will increase the significance level of the findings. Furthermore, another important limitation is due to the fact that we did not have access to the initial dataset from which AGB estimates in the Turtle Mountain were derived. As a result, it was not possible to examine the effect of the three factors of forest dynamics influencing changes in AGB after logging: mortality, growth and recruitment.

Nevertheless, based on the findings of Mazzei et al. (2010) the AGB recovery observed in the logged plot A was probably mostly due to the growth of the residual trees, particularly of the very large trees ($DBH \geq 70\text{cm}$). Moreover, Mazzei et al. (2010) found that tree recruitment into the 10 cm DBH class contributed relatively little to the increases in AGB over the early post-logging years but is expected to contribute more to AGB in the longer-run, as reported also by Blanc et al. (2009). On the other hand, the persistent decrease in AGB in the logged plot B was likely to be due to the high mortality rates of damaged trees, which typically continue for several years after logging (Durrieu de Madron, 1994; Silva et al., 1995; Sist & Nguyen-Thé, 2002; Blanc et al., 2009). It seems that unlike in the logged plot A, the AGB losses from these high mortality rates in plot B were not yet completely offset by the AGB gains due to tree growth. Moreover, Mazzei et al. (2010) found that plots with higher number of residual large tree showed higher overall AGB gains after logging because of the high rates of increase in AGB in very large trees ($DBH \geq 70\text{cm}$). Thus, a potential explanation for the observed differences in AGB changes between plot A and plot B could be partly due to differences in the number of very large trees in their residual forest, with plot A containing overall a higher number of very large trees than plot B which consequently resulted in higher AGB gain from tree growth.

In contrast to the logged plots, the AGB in the unlogged control plot was found to increase between 2002 and 2007 by 1.16 Mg/ha/yr. Unfortunately, AGB estimates for 2010 in the control plot are missing which limits the interpretation of this increase in AGB. However, this finding is similar to the mean AGB accumulation reported by Mazzei et al. (2010), Baker et al. (2004a) and Phillips et al. (1998) in undisturbed primary forests in the Amazon region. Furthermore, Mazzei et al. (2010) found that the overall AGB gains in secondary forests 2-4 years after selective logging were practically double of those in primary forests due to the high mean annual diameter increments of trees in the logged plots (2.6 Mg/ha/yr on average in secondary forest vs 1.4 Mg/ha/yr on average in primary forest). In addition, the study by Berry et al. (2010) in a tropical forest in Northern Borneo also reported a comparable high rate of AGB gains after

recent logging of 2.4 Mg/ha/yr. Therefore, the mean rate of AGB accumulation of 0.22 Mg/ha/yr in the Turtle Mountain 2-5 years post-logging is extremely low in comparison to the findings of Mazzei et al. (2010) and Berry et al. (2010).

When applying the rate of AGB accumulation defined by Mazzei et al. (2010) to the AGB data in the Turtle Mountain, the mean AGB in the logged forest was expected to recover to its initial value in about 35 years. In the Kaw Mountains, no conclusions could be made about the AGB recovery in the logged plots to its initial value due to the lack of data before logging occurred. However, more than 20 years were required for the mean AGB in its secondary forest to recover to a similar value contained in its primary forest in 2011, which could be regarded as a reference. The study by Blanc et al. (2009) showed that secondary forest sites in French Guiana under a higher logging intensity (10 stems per hectare) were expected to recover to their initial values in about 45 years. The longer time period expected for AGB recovery reported by Blanc et al. (2009) in comparison to our findings in the Turtle Mountain is likely to due to the higher logging intensity. Several studies have shown that higher logging intensities will significantly increase the time period for AGB recovery (Pinard et al., 1996; Putz et al., 2008; Mazzei et al., 2010).

However, the predictions made in this study about the temporal variation in AGB over the next 50 years should be treated with caution for several reasons. First of all, these predictions provide rough AGB estimates which do not include site specific characteristics. In this study, the rates of AGB accumulation reported by Mazzei et al. (2010) were used because they studied the effect of selective logging in a similar forest type and their results are more reliable due to their larger sample size. However, it is likely the AGB gains will differ slightly between the different forest sites because the effects of logging on forest dynamics (mortality, growth and recruitment) are site specific.

Secondly, the rate of AGB accumulation was assumed to remain constant, however, in practice the annual rate of growth is likely to decline as the forest matures resulting in lower rates of AGB accumulation (Berry et al., 2010). Therefore, the AGB recovery in the secondary forest in the Turtle Mountain is likely to require a longer time period than the predicted 35 years. Furthermore, since accumulation of biomass in primary forests cannot continue indefinitely, they should theoretically reach an equilibrium over the very long term. However, there is unequivocal evidence that the AGB of mature primary forests in the Neotropics is in fact still increasing (Harvey et al., 2009; Luyssaert et al., 2008; Mackey et al., 2008; Mahli & Phillips, 2011; Lewis et al., 2004; Rutishauser et al., 2010; Wright, 2005; Clark, 2007; Korner, 2009; Muller-Landau, 2009). A debate has arisen regarding the interpretation of this persistent biomass accumulation in intact primary forests. Two main hypotheses have been put forward: recovery from past disturbance or response to climate change. One hypothesis is that tropical forests that we consider as intact primary forests have actually suffered major natural or anthropogenic disturbances in the past, and are still in the process of recovery which is known as succession (Wright, 2005; Muller-Landau, 2009; Rutishauser et al., 2010; Mahli & Phillips, 2011). This hypothesis is supported by increasing palaeoecological and archaeological evidence proving that many of today's "intact" tropical forests actually have a long history of disturbances (Clark, 2007). The other hypothesis claims that the equilibrium of tropical forests has been shifted because of changes in resource availabilities driven by global climate changes. In particular, increasing CO₂ atmospheric concentrations is predicted to stimulate tree growth (Lewis et al., 2004; Korner, 2009; Phillips et al., 2008). However, if CO₂ atmospheric enrichment is the cause then trees are likely to reach CO₂ saturation levels at some point. There is a rising concern that the carbon sink in primary tropical forests will diminish and may eventually reverse to becoming a source due to higher respiration and higher mortality (Phillips et al., 2008; Malhi & Phillips, 2011). In conclusion, there are still many uncertainties about future changes in biomass within the context of climate change. Therefore, future research is needed to

carry out consistent monitoring of both primary and secondary forest dynamics which is crucial for improving future predictions of AGB and carbon stock changes.

4.5. Regional spatial variation in AGB across French Guiana

Despite observed variation in AGB between the 5 geographically different forest sites in French Guiana (Figure 10), these differences in AGB were found to be non-significant. Furthermore, no evidence of regional spatial patterns of AGB among these forest sites was detected from the multivariate analysis (Figure 12). The 5 forest sites studied are of similar Terra Firme forest habitat. Therefore, these findings suggest that the AGB in Terra Firme forests does not differ significantly across a regional scale within French Guiana. Consequently, general regional-scale AGB estimates for Terra Firme forests could be determined for French Guiana and used for comparison across larger expanses of the Amazon basin.

Several studies have shown that the AGB varies across the Amazonian forest along an east-west geographic gradient, with central and eastern Amazon forests having higher overall AGB estimates than in northwest or southwest Amazonia (Baker et al., 2004a; Malhi et al., 2006; Quesada et al., 2009; Baraloto et al., 2011). Therefore, comparisons of AGB within Terra Firme forest habitats across the Amazon basin would provide further information as well as improve our understanding of this east-west geographic gradient. For example, Baraloto et al. (2011) found that the average AGB in the Terra Firme forests in French Guiana was greater than in Loreto, Peru. There is no general agreement about the explanation for this spatial pattern in AGB across the Amazon. A positive feedback hypothesis in forest structure and turnover influencing AGB patterns in Amazonian forests is currently under discussion though. This hypothesis compares the eastern forests containing nutrient-rich fertile soils with higher turnover that supports small fast-growing trees with lower wood density vs. the western forests containing less fertile soils with lower turnover that supports many, larger slow-growing trees with denser wood (Van Schaik & Mirmanto, 1985; Quesada et al., 2009). In the same line of thought, Baker et al. (2004b) argued that spatial gradients in community wood density due to patterns of species composition across the Amazon strongly contributes to this spatial pattern in AGB, with eastern and central forests having 16% denser wood than western forests. In consequence, further investigation is needed to better understand the combination of factors influencing these large-scale patterns in AGB across the Amazonian forest. Last but not least, future studies should not only focus on estimating AGB within Terra Firme forest habitats across geographic regions in the Amazonian forest, but also among contrasting forest habitats both within and among these geographic regions (i.e. white-sand or seasonally-flooded forest habitats). This approach provides a more complete information and understanding of the potential differences in AGB across broad gradients of forest habitats and/or geographic regions.

4.6. The relationship between environmental factors with AGB

Despite no evidence for regional spatial variation in AGB in this study, the multivariate analysis provided information about the relationship between stand and climate variables with AGB. In general, the PCA results showed a strong relationship between AGB and stand variables. More specifically, the first principal component represented a gradient of increasing total AGB and AGB of big trees ($DBH \geq 10\text{cm}$) associated with increasing DBH, height, large stem density ($DBH \geq 30\text{cm}$) and stand basal area, vs. the second principal component represented a gradient of increasing AGB of small trees ($DBH \leq 10\text{cm}$) associated with increasing small stem density ($DBH \leq 10\text{cm}$; Figure 11). The first and second principal components were found to explain 36.58% and 21.45% of the variance in the dataset, respectively. This analysis underlines once more the important contribution of large trees ($DBH \geq 30\text{cm}$) to total AGB in comparison to small trees ($DBH \leq 10\text{cm}$), as discussed previously. Moreover, this strong relationship between AGB and stand variables is not surprising because diameter, height and wood density are used to estimate individual tree AGB. However, the positive correlation of total AGB with basal area and

large stem density ($\text{DBH} \geq 30\text{cm}$) was found to be stronger than with DBH, height and wood density (Appendix 7). These findings are consistent with other studies that also underline the importance of stem density and basal area for driving spatial variation in AGB estimates (Rutishauser et al., 2010; Slik et al., 2010). On the other hand, a weak correlation was found between total AGB and wood density. One possible explanation for the weak relationship between AGB and wood density in this study is due to the lack of broad gradients in wood density across the studied regions in French Guiana. Although Baker et al. (2004b) reported a positive correlation between wood density and AGB across broad gradients in wood density, other studies found no general relationship between AGB and wood density (Stegen et al., 2009; Baraloto et al., 2011). As a result, caution should be taken against generalizations of positive correlations between wood density and AGB, as this relationship may not be valid across all forest sites (Stegen et al., 2009; Baraloto et al., 2011).

Furthermore, the PCA results showed a weak relationship between climate variables with AGB. The contribution of climate variables to the first two principal components was very low. The third principal component was found to be a contrast between the climate variable associated with rainfall and the climate variable associated with dryness (DSI), which explained only 13.76% of the variance in the dataset (Appendix 8). Little research has attempted to investigate the relationship between climate and AGB which is probably due to the limited amount of precise climate data available across tropical forests. In general though, there appears to be a relationship between AGB and rainfall, with moist, stable (short dry season) climates supporting higher AGB in Panama, the Amazon, and Borneo (Chave et al., 2004; Malhi et al., 2006; Quesada et al., 2009; Slik et al., 2010). More specifically, this relationship was found to be the strongest during the dry season which supports the findings that AGB production depends especially on water availability when light and radiation are most abundant (Saleska et al., 2003; Malhi et al., 2006; Saatchi et al., 2007). However, the study by Baraloto et al. (2011) also reported a weak relationship between climate variables with AGB despite fine-scale characterization of climate regimes across broad habitat gradients. Furthermore, Quesada et al. (2009) showed that significant correlations between climate variables and AGB dissolved after correcting for spatial autocorrelation among the 59 Terra Firme forest plots in their study. Therefore, further research is necessary in order to determine the relative contribution of climate variables to spatial variation in AGB.

One important limitation in this study when examining the relationship between environmental factors with AGB is that soil and topographic variables as well as species composition and diversity information were not included into the analysis. The reason for this is due to the lack of high-quality data available describing these environmental factors for the different studied forest sites in French Guiana. Nevertheless, CIRAD and EcoFoG have planned to study the soil characteristics as well as identify all the different tree species present in our Gentry plots in the Kaw Mountains, with the objective to include this information in future studies. The Kaw Mountains are known to have a lateritic soil type which is likely to differ from the typical clay-rich soils in the other Terra Firme forests in French Guiana. Furthermore, CIRAD and EcoFoG so far have identified a distinct species composition in the Kaw Mountains which appears to be different to other forest sites in French Guiana, suggesting that the Kaw Mountains may represent an important natural refuge. Therefore, future comparisons between the Kaw Mountains and other Terra Firme forests across French Guiana may provide further information about the effect of species composition and soil fertility on AGB as well as forest structure and dynamics.

In conclusion, this study underlines the strong relationship between AGB and stand variables describing forest structure in Terra Firme forests across French Guiana. In contrast, this study did not uncover any strong relationship between AGB and climate variables. The inclusion of soil variables and biogeographic factors (i.e. species composition and topography) in future studies would improve our understanding of the complex relationship between environmental factors

with AGB. To be able to verify if these relationships between environmental factors and AGB are consistent across the Amazon basin, further investigation is necessary which covers broad environmental gradients. Baraloto et al. (2011) stress the importance that future studies attempting to link AGB with environmental factors must cover broad environmental gradients that can disentangle confounding effects among climate, soil, forest structure and other factors. In particular, they raise the issue that for most Terra Firme forest habitats, the east-west gradient in Amazonia represents a concomitant gradient of soil fertility, climate, wood density and forest turnover, making it complicated to test for the relative strengths of their relationships with AGB. Therefore, future research must identify major environmental gradients among various habitat types across the Amazon in order to be able to examine the relative contribution of each environmental factor to spatial patterns in AGB. Consequently, the results from this study do provide useful information that can be integrated with plot networks across the Amazonian forest in order to refine tests of the positive feedback hypothesis put forward to explain the spatial pattern in AGB across eastern-western Amazonian forests, as discussed earlier.

Finally, an important limitation in this study and previous studies is that stand variables were treated in the same manner as other environmental factors, despite the fact that they are directly or indirectly connected with the allometric equations used to calculate AGB. Baraloto et al. (2011) have suggested a hierarchical modeling framework to understand processes explaining spatial patterns in AGB. The first level of their analysis is based on the principle that higher AGB can only be achieved by increases in certain stand variables. Through their modeling approach, they examine the extent to which climate and soil explain spatial patterns in AGB and the extent to which they explain stand factors which in turn explain spatial patterns in AGB. Therefore, it is recommended for future studies to adopt this modeling framework developed by Baraloto et al. (2011). Especially since important practical implications towards mapping AGB at regional scales could be determined through this framework. For example, if climate and/or soil are significantly correlated with either AGB or stand variables that explain AGB, then spatial interpolation of these environmental data could be included into the models to map AGB. However, if this is not the case and only stand variables are found to be significantly correlated with AGB, then it would be more appropriate for modelers to focus on mapping stand structure, which could be derived from remote-sensing methods, without integrating environmental data. Despite limitations in this study, the results obtained are consistent with the results reported by Baraloto et al. (2011) which show that stand variables may prove to be valuable tools to estimate AGB. Future research is necessary to provide more evidence about the valuable role of stand variables as predictive variables to map and monitor forest AGB over the Amazon landscape. Furthermore, remote-sensing in this case would be a very promising instrument for estimating forest AGB and new technologies are currently being developed to strengthen its performance (Gibbs et al., 2007; Patenaude et al., 2005).

5. Conclusions & Recommendations

5.1. General outcomes in the Kaw Mountains

The total AGB in the three forest sites (primary Trésor, primary ONF and secondary ONF) in the Kaw Mountains ranged overall from 388.06 to 453.81 Mg/ha. These AGB values are comparable to those reported in other forest sites in French Guiana (Rutishauser et al., 2010; Baraloto et al., 2011) but are higher than the estimated Amazonian average of 288.6 Mg/ha (Malhi et al., 2006). Moreover, the AGB of big living trees (DBH \geq 10cm) was found to constitute most (93.3%) of the total AGB in the three forest sites in the Kaw Mountains in comparison to dead trees (3.9%), small living trees (DBH \leq 10cm; 2.1%) and lianas (0.6%). These findings are similar to those reported by Nascimento & Laurance (2002) during a study in primary Terra Firme Brazilian forest. Despite the apparent low contribution of dead trees, small trees and lianas to the total AGB, future studies should not systematically ignore them because they are known to play an important role in many aspects of forest dynamics and consequently they are likely to influence AGB and biodiversity patterns in tropical forests in the longer-term.

No clear evidence of local spatial patterns in AGB was found between the two Terra Firme primary forest sites in the Trésor Reserve and ONF area in the Kaw Mountains. Nevertheless, the distribution of trees within the different DBH classes did significantly differ between the two primary forest sites. To determine the potential reasons causing this difference in forest structure, further research should aim to investigate differences in species composition or succession stage between these forest sites. In addition, future studies should also attempt to estimate AGB in the other different forest types (i.e. savannas or flooded forests) and habitats (i.e. slope, hilltops or bottomlands) present in the Kaw Mountains, which would provide further information about potential spatial variation in AGB within the area.

Selective logging activity in the Kaw Mountains did appear to have a negative impact on forest AGB as lower AGB values were found in the secondary forest sites of ONF in comparison to both primary forest sites. However, this difference was found to be non-significant. Nevertheless, two important limitations may have influenced this non-significant result: low number of replicates and weak control for logging intensity.

When studying the forest structure, the logged forest in the ONF domain had a high total stem density (2348 trees/ha), low basal area (31.3 m²/ha) and high density of small trees, which are characteristics of secondary forests (Brown & Lugo, 1990). In particular, the distribution of trees within the different DBH classes was significantly different between secondary and primary forests because of the high density of very small trees (DBH \leq 5cm) in the secondary forest.

Finally, an interesting aspect which was not included in this study, due to incomplete field data, was the impact of logging activity on biodiversity patterns in the Kaw Mountains. Nonetheless, with the support of CIRAD and EcoFoG that are currently identifying the remaining unknown tree species, future studies will be able to include this data when investigating the effect of selective logging on biodiversity patterns while also attempting to link them with AGB patterns in the Kaw Mountains. It is of great importance to improve our understanding about how different components of biodiversity may influence AGB and carbon sequestration capacity for an effective implementation of REDD+ schemes.

To conclude, this research was the second step of a pilot-project for a multi-year REDD study. Therefore, follow-up studies will be able to make progress from these results in order to improve AGB estimates in the Kaw Mountains. Further research is necessary to provide a better understanding of the factors influencing variation in AGB in the area, which is relevant for future conservation of tropical forests under REDD+ in the Kaw Mountains.

5.2. Temporal variation in AGB due to selective logging activity

The similar AGB values found in both secondary forest sites in the Turtle Mountain and Kaw Mountains suggest that they may have encountered a similar amount of forest AGB damage due to recent selective logging. When comparing the AGB values before and two years after logging in the Turtle Mountain, AGB losses from felled and damaged trees were of about 87.11 Mg/ha, representing 19% of the estimated 454.42 Mg/ha prior to logging. Furthermore, the mean rate of AGB accumulation 2-5 years post-logging was 0.22 Mg/ha/yr, which is extremely low in comparison to other studies. Due to conflicting results between the two logged plots in the Turtle Mountain, no clear pattern of change in AGB could be defined. Therefore, increasing the number of replicates would improve the interpretation of patterns of changes in AGB after selective logging. In addition, future studies are also recommended to examine the effect of three important factors of forest dynamics on forest AGB (mortality, growth and recruitment) in order to understand the mechanistic driving these changes in AGB after logging.

Due to the limitations in this analysis, the mean rate of AGB accumulation defined by Mazzei et al. (2010) was used to predict changes in AGB over the longer-term. In the Turtle Mountain, the mean AGB in the logged forest was predicted to recover to its initial value in about 35 years. Despite the lack of AGB data prior to logging in the Kaw Mountains, the mean AGB in its logged forest was predicted to recover to a similar AGB values than in its primary forest in 2011 (used here as a reference) in about 20 years. However, these predictions in AGB recovery should be interpreted with caution because of two important limitations: the rate of AGB accumulation used did not include site specific characteristics and it was assumed to remain constant. To improve predictions, there is a need for further research to examine how the rate of AGB accumulation may change over time in both secondary and primary forests. In particular, further research is required to explain the unexpected persistent increase in AGB in primary tropical forests, which is currently under debate.

5.3. Regional spatial variation in AGB across French Guiana

Although there was variation in AGB between the 5 geographically different forest sites in French Guiana, no significant differences or regional spatial patterns in AGB were detected among these forest sites. Therefore, future studies could incorporate our findings when investigating potential regional spatial patterns in AGB across larger expanses of the Amazonian basin, as several studies argue that the Amazonian forest AGB may vary across an east-west geographic gradient (Baker et al., 2004a; Malhi et al., 2006; Quesada et al., 2009; Baraloto et al., 2011).

This research showed a strong relationship between AGB and stand variables describing forest structure in these forest sites, whereas a weak relationship between AGB and climate variables. Several other important environmental factors need to be included in future studies (i.e. soil and biogeographic variables) in order to provide further knowledge about the relative contribution of environmental variables to regional spatial patterns in AGB across the Amazonian forests. One important recommendation for future studies is that they must cover broad environmental gradients that can disentangle the confounding effects among these different environmental factors studied. A second recommendation is to use a hierarchical approach, as suggested by Baraloto et al. (2011), in order to treat appropriately stand variables from other environmental variables since these are directly or indirectly linked with AGB calculations. This would provide important implications for future mapping and monitoring of AGB in tropical forests, which is crucial for future REDD+ implementation. So far, our findings support Baraloto et al. (2011) conclusions that stand variables represent a valuable predictive variable for mapping AGB based on remote-sensing methods. Further research is needed to confirm and provide stronger evidence that this is the most appropriate approach for future landscape scale modeling of AGB in the Amazon.

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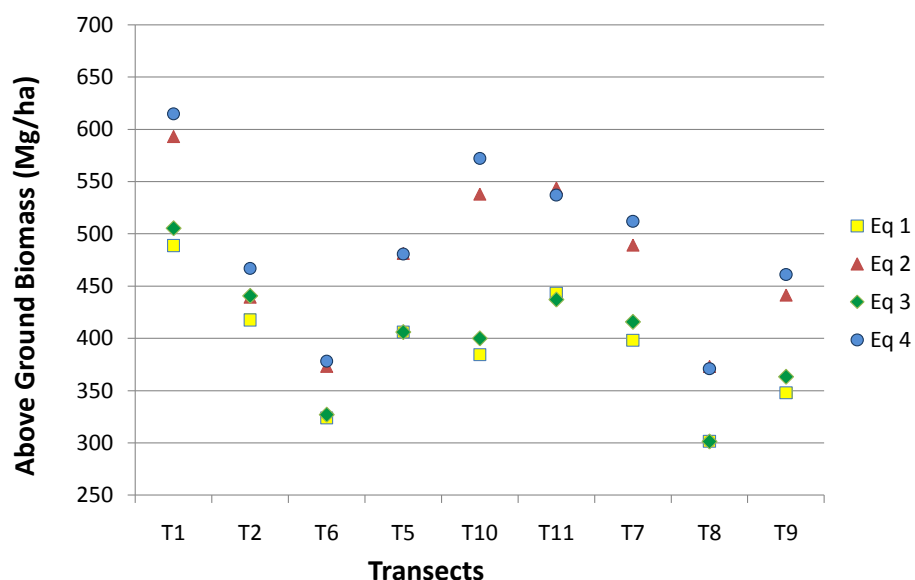
7. Appendix

Appendix 1: Map of French Guiana



Figure. Map of French Guiana. The studied forest areas are in green. Map modified from Source: U.S. Central Intelligence Agency, on www.geographicguide.net/america/french-guiana.htm (2010)

Appendix 2: The outcomes from different allometric equations



Eq 1: Chave et al (2005) with mean wsg and height
 Eq 2: Chave et al (2005) with mean wsg and without height
 Eq 3: Chave et al (2005) with specific wsg and height
 Eq 4: Chave et al (2005) with specific wsg and without height

Figure. Graph showing the above-ground biomass (Mg/ha) obtained from the four different allometric equations. Equation 1 (in yellow) is the Chave et al. (2005) equation with mean wood density (wsg) and height included. Equation 2 (in red) is the modified Chave et al. (2005) equation with mean wood density (wsg) and excluding height. Equation 3 (in green) is the Chave et al. (2005) equation with species specific wood density (wsg) and height included. Equation 4 (in blue) is the modified Chave et al. (2005) equation with species specific wood density (wsg) and excluding height.

Appendix 3: AGB data from the Turtle Mountain

Table. The AGB values (Mg/ha) in 2002, 2007 and 2010 of the three studied plots in the Turtle Mountain: logged plot A, logged plot B and control plot

Turtle Mountain	2002	2007	2010
AGB in logged plot A (Mg/ha)	471.93	381.31	390.26
AGB in logged plot B (Mg/ha)	436.90	353.31	345.69
AGB in control plot (Mg/ha)	400.60	406.40	

Appendix 4: Total mean AGB and associated percentages in the Kaw Mountains

Table. Total mean AGB values (Mg/ha) and associated percentages obtained by combining the three forest sites in the Kaw Mountains (Trésor Primary, ONF Primary and ONF secondary).

AGB categories (Mg/ha)	Kaw Mountains	Percentage (%)
AGB of big living trees (dbh≥10cm)	399.68	93.3
AGB of small living trees (dbh≤10cm)	9.13	2.1
AGB of dead trees	16.74	3.9
AGB of lianas	2.75	0.6
Total mean AGB	428.30	100.0

Appendix 5: Standardized residuals from the Chi-square test

Table. The standardized residuals obtained from the Chi-square test on the distribution of trees per hectare in the different DBH classes (cm). The absolute values of the standardized residuals greater than 2 are in bold.

DBH classes	Forest sites		
	Tresor Primary	ONF Primary	ONF Secondary
2.5 to 5 cm	-1.7929208	-1.78845606	3.3388539
5 to 10 cm	1.624585	0.13631758	-1.58512
10 to 20 cm	-1.2452978	3.25106234	-2.0410994
20 to 30 cm	2.7637754	0.04885258	-2.5190062
30 to 40 cm	1.5323134	-0.49501226	-0.8899762
40 to 70 cm	0.3989783	0.2477098	-0.5971714
70 cm and more	0.6933024	0.84045884	-1.4355697

Appendix 6: Mean AGB within the different DBH classes

Table. Mean AGB values (Mg/ha) and associated percentages in the different DBH classes for the three forest sites in the Kaw Mountains: Trésor Primary, ONF Primary and ONF secondary.

DBH Classes	Trésor Primary		ONF Primary		ONF Secondary	
	Mean AGB (Mg/ha)	Percentage (%)	Mean AGB (Mg/ha)	Percentage (%)	Mean AGB (Mg/ha)	Percentage (%)
2.5 to 5 cm	2.00	0.5	2.60	0.6	2.53	0.7
5 to 10 cm	7.52	1.7	9.32	2.2	7.33	2.0
10 to 20 cm	23.10	5.3	36.63	8.6	25.14	6.8
20 to 30 cm	46.24	10.7	39.90	9.4	31.60	8.5
30 to 40 cm	49.52	11.4	42.83	10.0	40.25	10.9
40 to 70 cm	136.75	31.5	146.88	34.4	142.37	38.5
70 cm and more	168.81	38.9	148.20	34.8	120.83	32.7
total	433.93	100.0	426.38	100.0	370.05	100.0

Appendix 7: Relationships between stand variables with total AGB

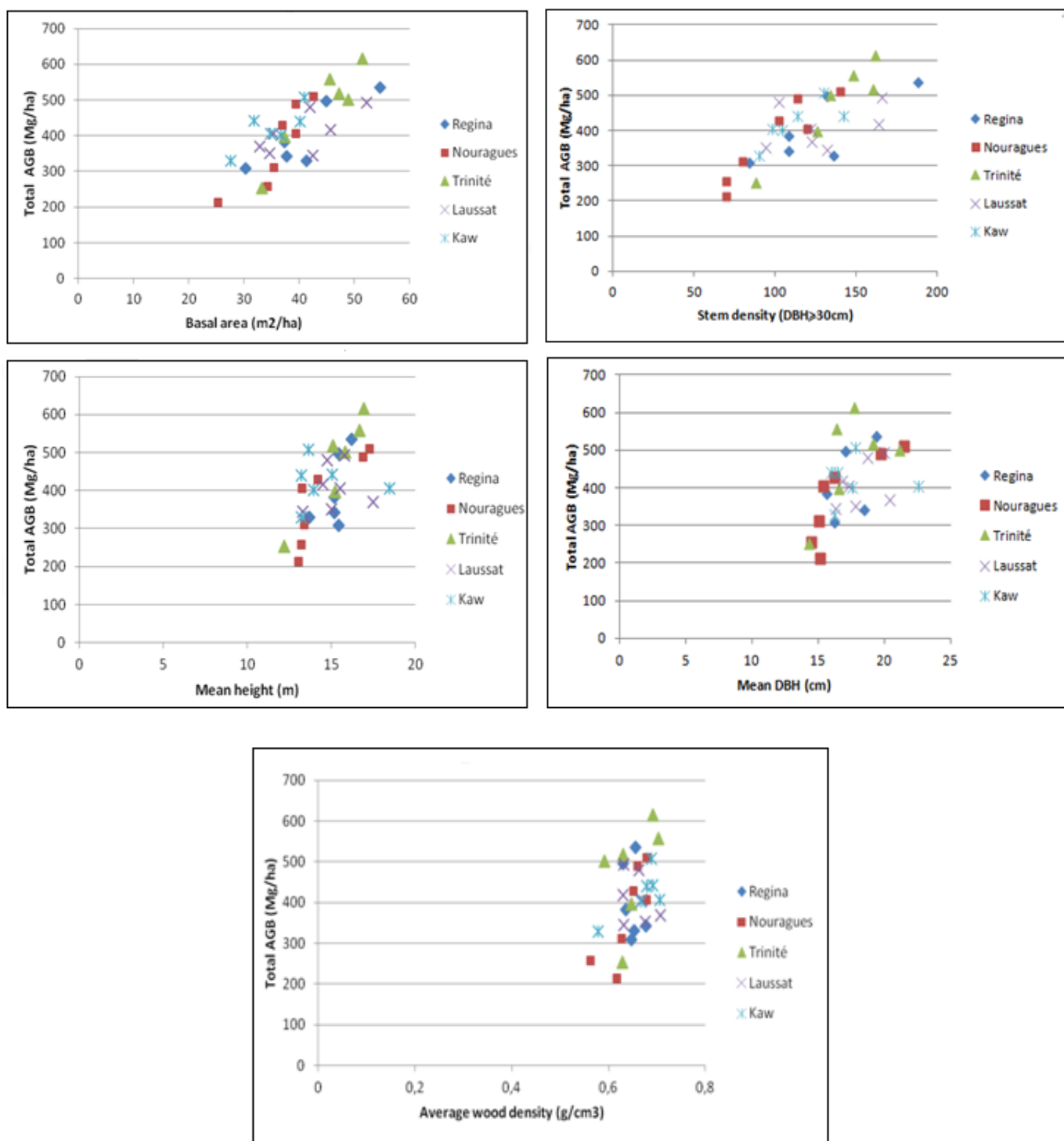


Figure. Selected relationships between total AGB (Mg/ha) and stand variables: basal area (m²/ha), stem density (DBH ≥ 30 cm), mean height (m), mean DBH (cm) and average wood density (g/cm³). The graphs show the results for the five different forest sites in French Guiana: Regina (blue diamond), Nouragues (red square), Trinité (green triangle), Laussat (black cross) and Kaw (blue cross).

Appendix 8: Graph of PC3 vs PC4

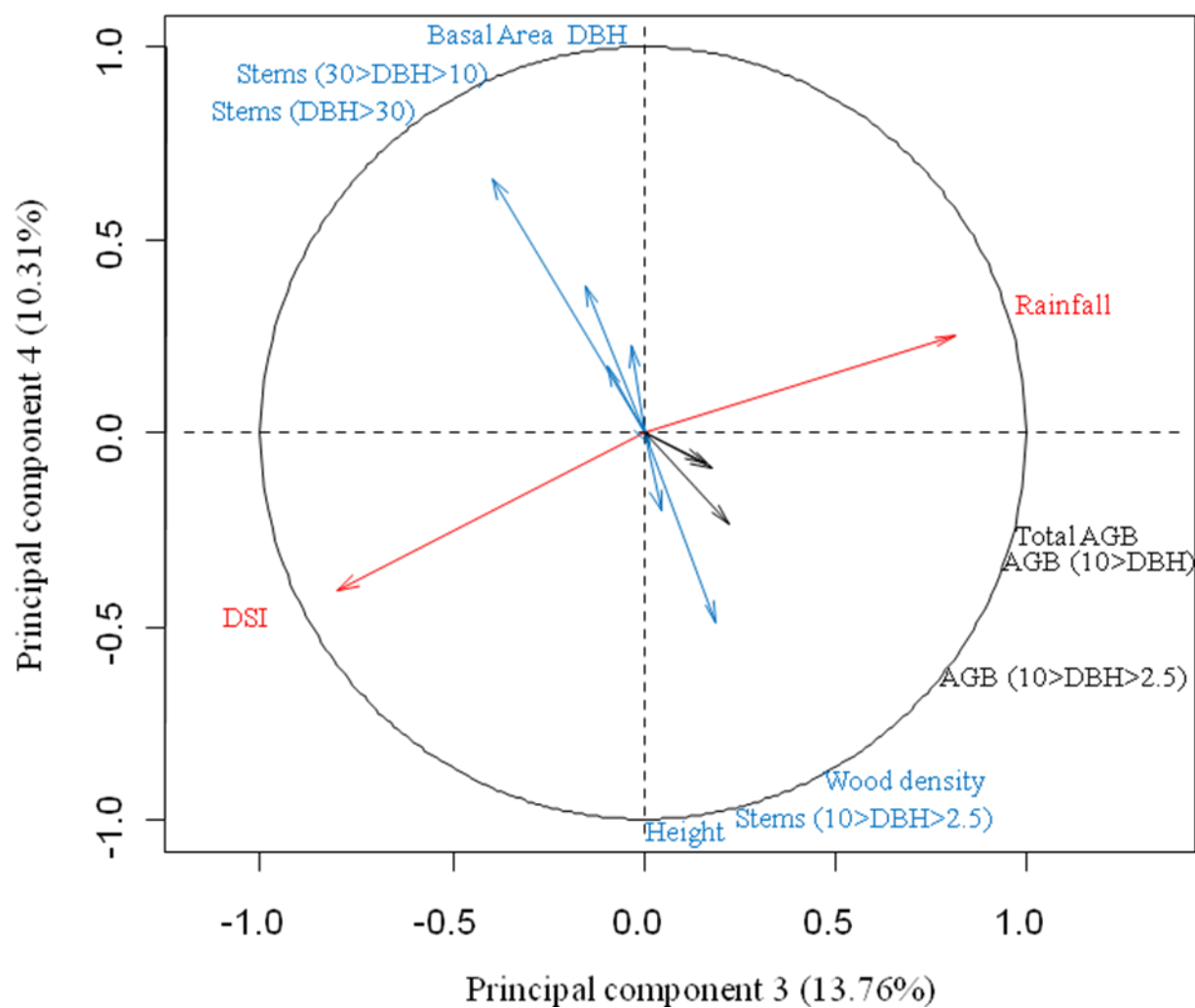


Figure. Graph representing the contribution of the twelve different variables towards Principal component 3 (explaining 13.76% of the variation in the dataset) against Principal component 4 (explaining 10.31% of the variation in the dataset). The stand, climate and AGB variables are illustrated respectively in blue, red and black.

Appendix 9: Summary R script

The R script used to calculate the AGB with the different allometric equations is given below. The rest of the R script used for the statistical analysis can be provided upon request.

R SCRIPT:

```
# List of files
```

```
list.files ()  
library(FactoMineR)
```

```
# Import data for dead wood - datadead
```

```
dead=read.table("deadtree.csv", header=TRUE, sep=";", dec=".", na.strings="")
```

```
# Calculate dbh for dead wood
```

```
unknown=is.na(dead$dbh)  
dead[unknown,]$dbh=dead[unknown,]$circ/pi
```

```
# Calculate the AGB per transect of dead wood using allometric equation of Baker et al.  
(2007)
```

```
datadead=dead[dead$include,c(1, 6, 8)]  
datadead$AGB=(0.0509*(0.4*datadead$dbh^2*datadead$height))*0.5
```

```
tra=levels(datadead$Transect)  
resdead=c()  
for(i in 1:length(tra)){  
  AGBtemp=datadead$AGB[datadead$Transect==tra[i]]  
  AGBtra=sum(AGBtemp)  
  resdead=c(resdead, AGBtra)  
}  
resdead=resdead/(1000*0.5)  
names(resdead)=tra  
resdead
```

```
# Import living tree and liana data
```

```
data=read.table("Livingtree.csv", header=TRUE, sep=";", dec=".", na.strings="")
```

```
# Calculate unknown dbh for living trees and lianas
```

```
unknown=is.na(data$dbh)  
data[unknown,]$dbh=data[unknown,]$circ/pi
```

```
# Select liana data - biomassliana
```

```

biomassliana=data[data$dbh>=10 & data$Liana,c(1, 7)]

# Calculate the AGB per transect of lianas using the allometric equation of Schnitzer et
al. (2006)

biomassliana$AGB=exp(-1.484+2.657*log(biomassliana$dbh))

tra=levels(biomassliana$Transect)
resliana=c()
for(i in 1:length(tra)){
  AGBtemp=biomassliana$AGB[biomassliana$Transect==tra[i]]
  AGBtra=sum(AGBtemp)
  resliana=c(resliana, AGBtra)
}
resliana=resliana/(1000*0.5)
names(resliana)=tra
resliana

# Select binomial data of living trees

data$bin=as.factor(paste(as.character(data$GEN), as.character(data$SP)))

# Calculate the AGB per transect of big living trees using the allometric equation of
Chave et al. (2005) including mean wood density and height - biomassliving1

biomassliving1=data[data$dbh>=10 & !data$Liana & !data$Palm, c(1, 7, 8)]
biomassliving1$AGB=0.0509*0.66*biomassliving1$dbh^2*biomassliving1$height

tra=levels(biomassliving1$Transect)
resliving1=c()
for(i in 1:length(tra)){
  AGBtemp=biomassliving1$AGB[biomassliving1$Transect==tra[i]]
  AGBtra=sum(AGBtemp)
  resliving1=c(resliving1, AGBtra)
}
resliving1=resliving1/(1000*0.5)
names(resliving1)=tra
resliving1

# Calculate the AGB per transect of big living trees using the allometric equation from
Chave et al. (2005) with mean wood density and excluding height - bmliving1

bmliving1=data[data$dbh>=10 & !data$Liana & !data$Palm, c(1, 7, 8)]
bmliving1$AGB=0.66*exp(-1.499+2.148*log(bmliving1$dbh)+0.207*
log(bmliving1$dbh)*log(bmliving1$dbh)-0.0281*log(bmliving1$dbh)*
log(bmliving1$dbh)*log(bmliving1$dbh))

tra=levels(bmliving1$Transect)

```

```

resbmliving1=c()

for(i in 1:length(tra)){
  AGBtemp=bmliving1$AGB[bmliving1$Transect==tra[i]]
  AGBtra=sum(AGBtemp)
  resbmliving1=c(resbmliving1, AGBtra)
}
resbmliving1=resbmliving1/(1000*0.5)
names(resbmliving1)=tra
resbmliving1

# Import wood density DryadChave database

wsgdata=read.table("wsgdatabase.csv", header=TRUE, sep=";", dec=".", na.strings="")

# Calculation of mean wood density in DryadChave database

wsgdb=by(wsgdata$wsg, wsgdata$Binomial, mean) # calculation of mean wsg
wsgbin=c() # mean wsg per binomial
for(i in 1:length(wsgdb)){
  wsgbin=c(wsgbin, wsgdb[i])
}

wsgbin=cbind.data.frame(names(wsgbin), wsgbin)
names(wsgbin)=c("bin", "wsg")

# Assign wood density per binomial for livingtree data

data=merge(x=data, y=wsgbin, all.x=TRUE, all.y=FALSE)
summary(data)

# Calculate the AGB per transect of big living trees using the allometric equation of
Chave et al. (2005) with species specific wood density and height included-
biomassliving2

biomassliving2=data[data$dbh>=10 & !data$Liana & !data$Palm, c(2, 8, 9, 15)]
biomassliving2$AGB=0.0509*biomassliving2$wsg*biomassliving2$dbh^2*biomassliving2$height

tra=levels(biomassliving2$Transect)
resliving2=c()

for(i in 1:length(tra)){
  AGBtemp=biomassliving2$AGB[biomassliving2$Transect==tra[i]]
  AGBtra=sum(AGBtemp)
  resliving2=c(resliving2, AGBtra)
}
resliving2=resliving2/(1000*0.5)

```



```
names(resliving2)=tra
resliving2
```

```
# Calculate the AGB per transect of small living trees using the allometric equation of
Chave et al. (2005) with species specific wood density and height included-
biomassliving2
```

```
biomasslivingS2=data[data$dbh<=10 & !data$Liana & !data$Palm, c(2, 8, 9, 15)]
biomasslivingS2$AGB=0.0509*biomasslivingS2$wsg*biomasslivingS2$dbh^2*biomassli
vingS2$height
summary(biomasslivingS2)
# calculation of biomasslivingS2 per transect
tra=levels(biomasslivingS2$Transect)
reslivingS2=c()
```

```
for(i in 1:length(tra)){
  AGBtempS=biomasslivingS2$AGB[biomasslivingS2$Transect==tra[i]]
  AGBtraS=sum(AGBtempS)
  reslivingS2=c(reslivingS2, AGBtraS)
}
reslivingS2=reslivingS2/(1000*0.1)
names(reslivingS2)=tra
reslivingS2
```

```
# Calculate total AGB per transect of living trees using the allometric equation of Chave
et al. (2005) with species specific wood density and height included - reslivingTOT
```

```
biomasslivingtot=data[!data$Liana & !data$Palm, c(2, 8, 9, 15)]
biomasslivingtot$AGB=0.0509*biomasslivingtot$wsg*biomasslivingtot$dbh^2*biomass
livingtot$height
summary(biomasslivingtot)

tra=levels(biomasslivingtot$Transect)
reslivingtot=c()
```

```
for(i in 1:length(tra)){
  AGBtemptot=biomasslivingtot$AGB[biomasslivingtot$Transect==tra[i]]
  AGBtratot=sum(AGBtemptot)
  reslivingtot=c(reslivingtot, AGBtratot)
}
reslivingtot=reslivingtot/(1000*0.5)
names(reslivingtot)=tra
reslivingtot
```

```
# Calculate the AGB per transect of big living trees using the allometric equation of
Chave et al. (2005) with species specific wood density and excludingout height -
bmliving2
```

```

bmliving2=data[data$dbh>=10 & !data$Liana & !data$Palm, c(2, 8, 15)] #select big trees
and exclude lianas & palms
bmliving2$AGB=bmliving2$wsg*exp(-
1.499+2.148*log(bmliving2$dbh)+0.207*log(bmliving2$dbh)*log(bmliving2$dbh)-
0.0281*log(bmliving2$dbh)*log(bmliving2$dbh)*log(bmliving2$dbh))

tra=levels(bmliving2$Transect)
resbmliving2=c()

for(i in 1:length(tra)){
  AGBtemp=bmliving2$AGB[bmliving2$Transect==tra[i]]
  AGBtra=sum(AGBtemp)
  resbmliving2=c(resbmliving2, AGBtra)
}
resbmliving2=resbmliving2/(1000*0.5)
names(resbmliving2)=tra
resbmliving2

```