Structural Changes are More Important than Compositional Changes in Driving Biomass Loss in Ugandan Forest Fragments

C. Bulafu[1*], D. BarangA[1], A. E. Eycott[2], P. Mucunguzi[1], R. J. Telford[2], and V. Vandvik[2]

[1]*Department of Biology, School of Natural Sciences, Makerere University, P. O. Box 7062 Kampala, Uganda.*
[2]*Department of Biology, University of Bergen, Thormøhlensgate 53A, N-5006 Bergen, Norway*

Date Received: 16-08-2013 Date Accepted: 16-11-2013

Abstract

Aboveground biomass (AGB) contained in privately-owned forests is less frequently measured than in forest reserves despite their greater likelihood of degradation. We demonstrate how density changes in contrast to species compositional changes have driven AGB changes in privately-owned fragments in Uganda over two decades. Data on tree assemblages in fragments were obtained by re-sampling a 1990 dataset in 2010 and AGB estimated using generalised allometric equation that incorporates diameter at breast height (DBH) and species-specific wood density. AGB were highly variable between fragments and over time. Structural changes contributed a higher proportion of change in AGB than species compositional changes in all forests. Non-pioneer species constituted over 50% of AGB in reserve forest, in contrast to private forests where pioneer species dominated. Our study demonstrates the potential of private forests to hold comparable AGB to plantation. Reduction in exploitation pressure is required if fragments are to mitigate carbon emissions.

Keywords: *REDD+, Kampala, Re-sampling, Non-pioneer, Carbon markets*

1. Introduction

The rate of tropical forests loss, both through deforestation and degradation, is mostly driven by human activities such as land use change and wood extraction (IPCC, 2007). In Africa, the role of human activities in these declines shows no signs of abating (MEA, 2005; Schleuning *et al*., 2011). Deforestation, mainly due to conversion of forests to agricultural land, shows signs of decreasing and in tropical Africa it is currently 3.4 million hectares annually and contributes to between 12 and 20% of anthropogenic carbon emissions (FAO, 2006; FRA, 2010). In addition to deforestation however, degradation in the form of selective logging in both public and private forests is becoming a dominant form of land use change in Africa, and large parts of forested areas have been impoverished by this direct form of human activity (Asner *et al*., 2004). Despite the clear expectation that degradation pressures varies among public and private forests and that it leads to short and long lived effects on ecosystem processes and functions (MEA, 2005), few studies have contrasted private urban and public forests. For instance, the likely alteration of forest potential for carbon storage due to degradation is not completely understood yet. Thus based on current projections of forest degradation there is a need to examine how different components of degradation affect ecosystem processes that sustain the provisioning of goods including carbon storage and services to society.

Forest degradation can be considered as two separate components: firstly timber volume loss through harvesting, which leads to structural changes (tree size and density change) when particular size classes are selected, and secondly species compositional changes which involve shifts from non-

[*] *Correspondence: collinsabc@gmail.com*
Tel: +256776846216
ISSN 2235-9370 Print / ISSN 2235-9362 Online

pioneer to pioneer species in response to selective logging (Oliveira *et al*., 2004). Both components can impact forest carbon storage and other ecosystem services. The pioneer species typically have lower wood density and thus retain less carbon per capita than non-pioneer old growth species (Tabarelli *et al*., 2008). Both forest structural and species compositional changes towards pioneer species are thus driven mainly by anthropogenic disturbance including logging, firewood production and other extractive activities. Partitioning AGB change into these two components is necessary to understand the dimensions of the most important drivers of AGB change and thus develop a set of sound indicators that can provide meaningful assessment for effective management interventions aimed at maintaining or increasing carbon sequestration in forest fragments.

Studies that contrast public and private forests have shown that private forests are under the greatest threats and suffer the highest structural and compositional changes (Bulafu *et al*., 2013; Naughton-Treves *et al*., 2005) and that AGB heavily depends on size class frequency where intermediate-sized (20–50 cm DBH) stems accounted for 46.7% of total AGB (Nascimento and Laurance, 2002). We predict that differences in protection status will lead to high AGB loss, which will be driven mainly by forest structural changes, in private forests with low control on access rights compared to public forests. We therefore consider the roles of forest structure (i.e. volume changes) and species composition (i.e. species turnover) in determining the variation in AGB between private and public forests. Specifically we analysed: (i) the variation in AGB between forests and the effect of disturbance and protection status ii) temporal AGB changes among forests by size classes, successional status: non-pioneer and pioneer species (iii) AGB change due to volume and species turnover and iv) estimate AGB for dominant species among forests. Inventorying changes in AGB and carbon stocks will contribute to understand the role of forests fragments in global carbon cycles and management of existing AGB on land for GHG emission mitigation (Munishi, 2004).

2. Materials and Methods

2.1 Study sites

The study was carried out in the greater Kampala area in central Uganda (0º 05'N–0º 16'N, 32º 30'E–32º 38'E). The area consists of type C2 *Piptadeniastrum-Albizia-Celtis* forests whose sizes ranged from 5 to 476 hectares (Appendix 1) that extends over gently undulating land between 1200–1250 m altitude mainly (Langdale-Brown et al., 1964). The region has annual mean rainfall 1350 mm with bimodal pattern, and annual mean temperature of 25°C (NEMA 2007). Twenty two fragments in our study area were originally surveyed by Baranga in 1990 (Baranga, 2004). Out of these, only 11 forests remained at the time of this repeat survey in 2010 (Bulafu *et al*., 2013). The forests are interspersed within a matrix of agricultural areas (coffee-banana-sweet potatoes), cattle paddocks, human habitations and infrastructural developments.

To address temporal changes in AGB, we re-sampled remnant forests: three government owned (public) forests (A, B and C) and eight privately owned forests (D – K; Baranga, 2004). Forest (A) is the nearest reserved forest to the fragments located about 28 km inland from the shore of Lake Victoria, managed by National Forestry Authority and was included for comparative purposes. It is classified as a medium altitude moist evergreen forest about 450 ha of type C2 *Piptadeniastrum-Albizia-Celtis* forest (Dawkins and Philip, 1962). Forest (B) is managed by Coffee Research Institute located inland and consists of naturally regenerating cocoa and tea experimental plots abandoned fifty years ago. Eggeling, (1940) provided a detailed description of Forest (C) managed by Uganda Virus Institute and located near the shores of Lake Victoria. Four church owned forests (D, E, F and G); three forests owned by private individuals (H, I and J); and one sacred forest controlled and managed by a local community (K) (Figure 1) constituted the eight private forests located on private land that are not protected by national law. Four of the private forest fragments (D-G) were part of the once extensive lake shore forests of the Entebbe Peninsula on the heavily indented northern coastline of Lake Victoria, and are less than 3 km apart (Figure 1). Over the entire survey period, ownership type did not change for any of the fragments.

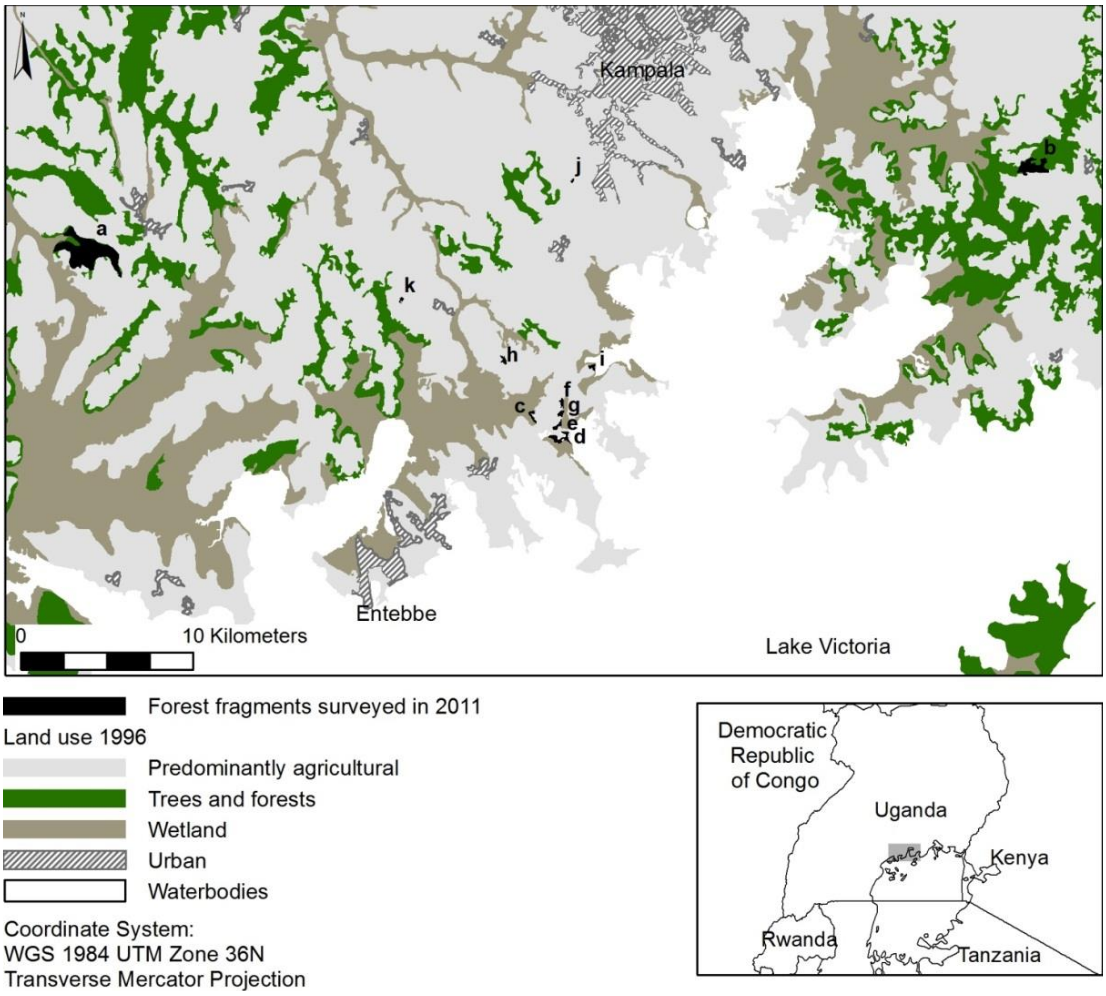

Figure 1: Map showing location of the study area and forest fragments.

1.2. Field measurements

Only trees plots minimum diameter at breast height (DBH) of ≥ 3.7 cm measured at 1.3 m above the ground rooted within 10 × 5 m plots established along the transects at 50m intervals were included in the original survey in 1990 and in the present survey (Baranga, 2004). For each forest fragment, line transects were established parallel to the longest axis and whose length ranged from 100 to 1000 m depending on forest size and started 10 m from the edge of the fragment. Neighbouring transects were separated from each other by 30m. In forest A, transects were set along the already established trail system in a north-south direction but excluding swamp forest stands. The number of transects established and plots sampled are indicated in Appendix 1.

Diameter at reference height (DRH) above the buttress was measured for species with buttresses higher than the breast height (Sheil *et al*., 2000). Tree stumps were enumerated in 10 × 5 m plots in each forest. Tree basal area loss was calculated using DBH of the stumps as an index of biomass outtake. Nomenclature followed Hamilton (1981). Voucher specimens are held at Makerere University Herbarium. Palms encountered in this study were omitted from the analysis as they were not enumerated in the 1990 survey.

Scores from 1 to 4 were used to assess disturbance status of the forest fragments (1 - fairly intact; 2 - disturbed; 3 - degraded, 4 - highly degraded) as follows: (1) presence of a distinct upper and middle canopy, with low density of undergrowth; (2) presence of a distinct upper, middle canopy, with high density of undergrowth; (3) presence of a distinct upper and middle canopy with high number of gaps and evidence of human activities such as tree cutting and forest clearing and (4) presence of only one distinct upper canopy, no or low undergrowth and high number cut trees (Figure 5). Level of protection was categorised as strict if a guard was employed (Forests A-C and I-J,) or weak if no guard was employed by the forest owners (Forests D-H). For simplicity species were classified into two ecological groups, whose members share characteristics of importance for determining structure and composition: (i) non-pioneer (ii) pioneer species following (Lwanga, 2003). A third category (unknown) was reserved for unidentified species. This classification allows for some generalizations and comparisons. However, we recognize that there might be other subdivisions e.g. (i) shade-tolerant tree species of the lower woody strata of primary forest; (ii) light demanding, relatively long-lived species; (iii) relatively short-lived species requiring gaps for germination and establishment all of which were present in the dataset. Forest areas were calculated from shapes delineated from 2010 aerial photographs and comparing with LANDSAT images of both 2010 and 1990 (30 m spatial resolution TM composites) in ArcGIS 10.0.

1.3 AGB and carbon calculations

AGB here is used to represent only the above-ground portion of live trees ≥ 3.7 cm DBH and excluding palms, vines, litter, dead trees and roots. AGB was estimated for each stem with the commonly used moist forest AGB equation (Chave *et al*., 2005). Data on stem DBH and woody density at genus/species level were incorporated into the allometric equation for AGB estimations as adopted by Alves *et al*., (1997). We used a generalised allometric equation for moist forest stands incorporating DBH and species specific values of wood density to estimate AGB (Chave *et al.,* 2006):

$$(AGB)_{est} = \rho \times \exp(-1.499 + 2.148 \ln(DBH) + 0.207 (\ln(DBH))^2 - 0.0281 (\ln(DBH))^3)$$

Where: ρ is wood density (gcm^{-3}).

Species-specific wood densities were taken primarily from the UN Food and Agricultural Organisation and World Agroforestry's Wood Density Database, supplemented by the PROTA database www.worldagroforestry.org/Sea/Products/AFDbases/wd/ (following Chave *et al*., 2006). For species with unknown wood density, the mean wood density of all species of the same genus found in the literature search was used, as genus is a good predictor of species wood density (Chave *et al*., 2006). We used AGB generated from the above equation to estimate its variation between forests by: i) size class as follows: mature trees > 40cm DBH; adult trees 20-40; young trees 10-20; and saplings < 10 and ii) by successional status i.e. non-pioneer and pioneer species.

To investigate the main mechanisms driving AGB changes in the forests, we partitioned AGB change into structural, compositional and total change as follows:

$$\delta V = v10 \times d90 - v90 \times d90;\ \delta D = v90 \times d10 - v90 \times d90;\ \delta AGB = v10 \times d10 - v90 \times d90$$

Where δV is change due to structural (volume) differences only; δD is change due to species compositional differences (density) only; δ AGB is total AGB change. v10 and v90 are volume in 2010 and 1990 sample regimes respectively; d10 and d90 are weighted mean wood densities of species in 2010 and 1990 sample regimes respectively. To investigate the effects of level protection, disturbance index on AGB, we used non-parametric Kendall’s rank correlation tau test.

Forest AGB standard errors (SE) were calculated as standard deviation divided by the square root of the sample size. Finally, tree AGB was converted into carbon through multiplication by 0.5 (moist forest equation, Chave et al., 2005). Data preparation and AGB analyses were performed using the R statistical language version 3.0.1 (R Core Team, 2013).

3. Results

In 1990, forests showed high variability in the amount of AGB, ranging between 99.6 ± 11 t ha^{-1} and 68.6 ± 9 t ha^{-1} in public forests and between 55.3 ± 8 t ha^{-1} and 95.1 ± 11 t ha^{-1} in private forests while in the current survey AGB ranged between 91.7 ± 11 t ha^{-1} and 83.2 ± 9 t ha^{-1} in public forests and between 21 ± 15 t ha^{-1} and 83 ± 9 t ha^{-1} in private forests (Figure 2a). We found that AGB decreased with an increase in disturbance index (Kendall's Tau = -0.674, P = 0.01) while AGB increased with protection status Kendall's Tau = 0.713, P = 0.01). AGB differences were seen when comparing tree size distribution in forest fragments or when comparing species ecological successional status (Figures 2 a & b). Large trees (DBH > 40 cm) contributed between 40-46% of total AGB in our forests fragments, while the small trees (< 10 cm DBH) contributed between 8-13% of total AGB. Non-pioneer species constituted the greatest amount of AGB in the public forests while in private forests, pioneer species held the most AGB (Figure 2b). Biomass removal in the current survey showed idiosyncratic trends across size classes with highest removal taking place in the private forests (Figure 3).

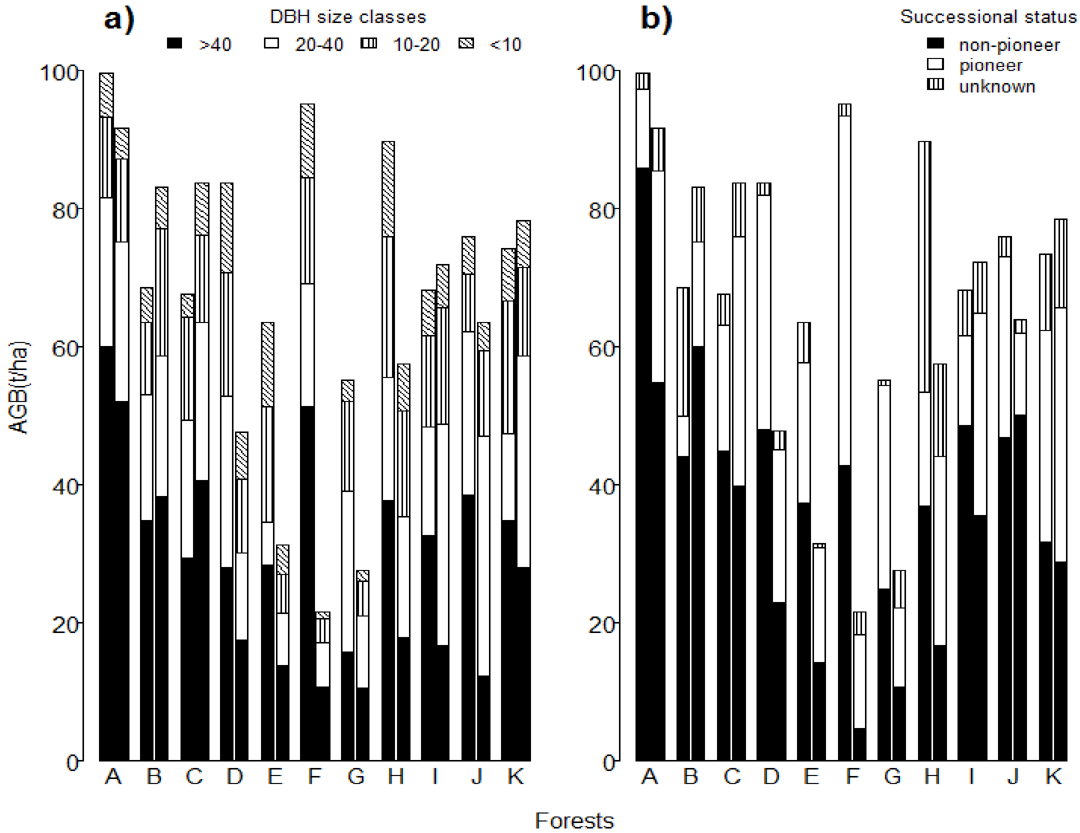

Figure 2: AGB (t ha-1) estimates per DBH size class (cm) from allometric equation for forest fragments in Kampala area divided by (a) DBH size classes and (b) successional status. (Full names for sites A-K can be found in Table 1)

Over time, there were high declines in the amount of AGB in several of the forests. For example, private forests, particularly church forests E, F and G, had the highest declines in the amount of AGB, losing between 40 and 77% (Figure 2a). Public forests showed minimal declines (Figure 2a forest A) or slight increases in amount of AGB stored over the two decades, particularly in large sized trees (Figure 2a forests B and C). Over two decades, biomass change generally showed idiosyncratic trends across size classes (Figure 2a). Forests I, J and K show compensatory growth in that AGB decreased in large-trees, yet in intermediate-sized trees (DBH cm 20-40) AGB increased (Figure 2a), The highest proportion of change in AGB was due to structural changes with species compositional changes playing a minor role, particularly in church forests (Figure 4). The covariance, which relates to unequal representation of species across size classes, represented a small fraction of AGB change across forest fragments (Figure 4).

Considering the top five species contributing to the most AGB across forests, no single species was consistently among the five species of highest per-hectare AGB across forests. Within forests, the species with the highest AGB were not exactly the same five species for each time period. Overall, in the non-pioneer successional status group, Trilepisium madagascariense DC., Pseudospondias microcarpa (A.Rich.) Engl., Antiaris toxicaria (Rumph.ex Pers.) Lesch., Sapium ellipticum (Hochst.ex Krauss) Pax and Manilkara butugi Chiov held 66% of AGB while Maesopsis eminii Engl., Piptadeniastrum africanum (Hook.f.)Brenan, Erythrophleum suaveolens (Guill. & Perr.) Brenan, Pycnanthus angolensis (Welw.) Warb., and Artocarpus heterophyllus Lam. , held 64% of the AGB in pioneer successional group (Appendix 2).

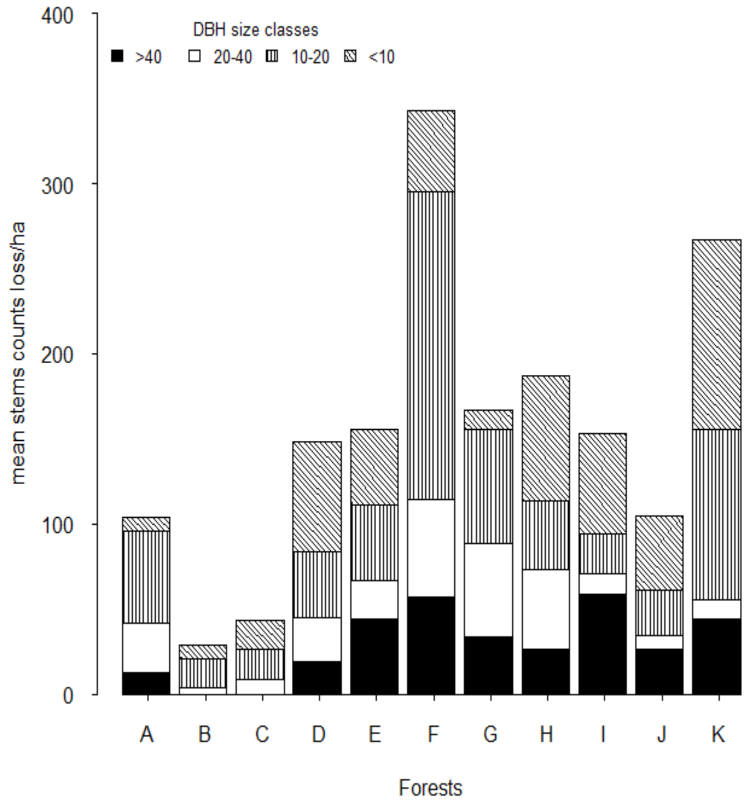

Figure 3: Distribution of biomass removal (mean stems/ha) per DBH size class (cm) in Kampala forest fragments for the current survey.

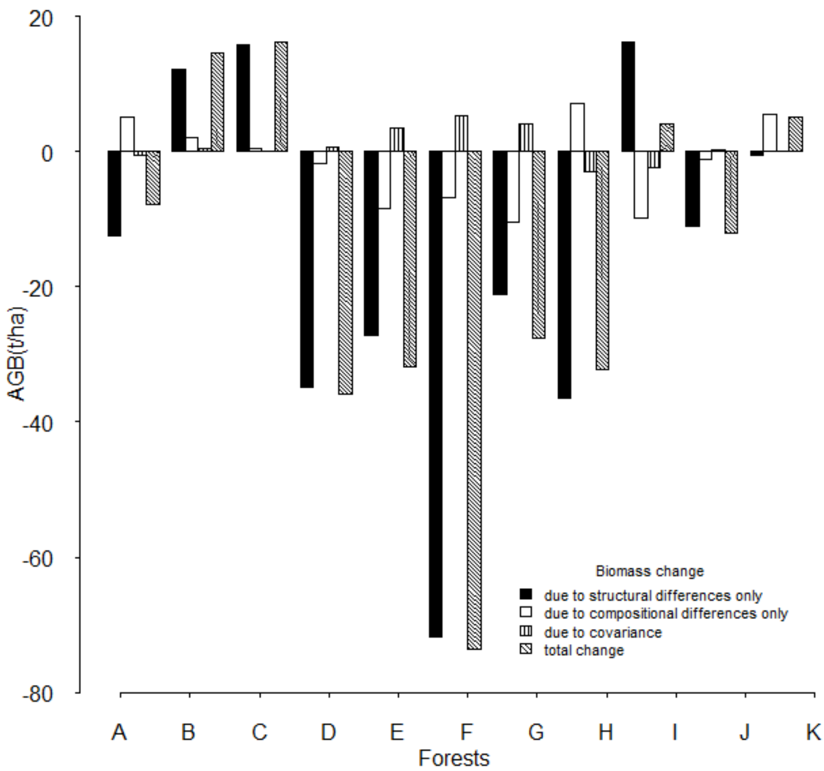

Figure 4: Change in AGB (t ha^{-1}) due to volume and density changes over two decades for forest fragments in Kampala area. (Full names for sites A-K can be found in Table 1)

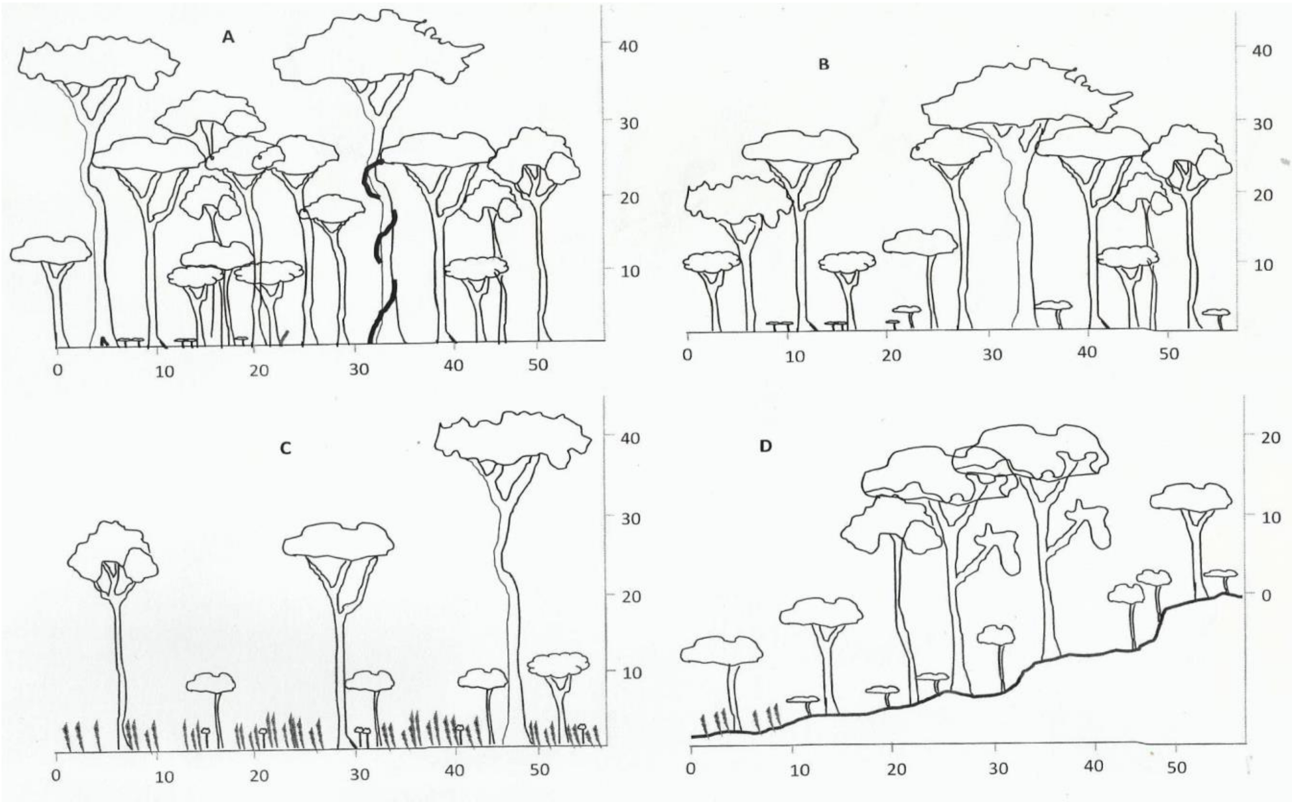

Figure 5: Profile diagram of forest fragments in 2010 for: A) Government forest A; B) Private forest H; C) Church forest F and D) Sacred forest K. For forest codes see Table 1.

4. Discussion

Aboveground biomass varied strongly between forest fragments under different protection levels and ownership, with public-owned forest holding the highest AGB. We additionally found a considerable reduction in AGB (and consequently in carbon) over time in privately-owned forests, mainly driven by structural changes in the forests and particularly by significant reductions in stem densities over the two decades in the four size classes investigated.

Furthermore, large trees contained the majority of AGB, our results showed that the importance of medium-sized trees in compensating for loss of large trees in some of the private fragments. In private forests, biomass removal showed idiosyncratic trends across size classes. Our forest fragments are in the same climatic region and thus variations in abiotic factors such as soil, rainfall and temperature are too small to have a major effect on AGB changes reported here. Elsewhere these factors have been shown to have small or no explanatory power for the AGB patterns (Tabarelli et al., 2010; Baraloto et al., 2011). Human related disturbance in the form selective logging and fragmentation effects seem to be the prominent factors responsible for the observed variation between forests and over time.

In our study sites, the public forests stored more AGB and were less affected by structural changes than the more disturbed, private or smaller forest fragments which were under high extraction pressure thus experienced high structural changes. Generally, compositional changes played a minor role in the AGB changes in our study systems.

The forest reserve estimates compare well with those reported elsewhere for similar tropical high forests at normal stocking densities associated with the moist lowland agro-ecological zone of Uganda, which ranged between 80 and 180 t ha-1 (Drichi, 2003) and other moist forest types elsewhere in Africa, e.g. 120-135 t ha-1 in Mozambique and 140 t ha-1 in Gambia (Brown, 1997). The high values of AGB in reserved forests can be attributed to low changes in stem density (low structural changes), relatively high density of large trees akin to intact mature forest with minimal anthropogenic disturbances. Forest types with larger trees have been shown to accumulate more AGB hence more carbon (Munishi, 2004). In the private forests, the high volume changes resulted in massive AGB declines and we attributed this to high biomass extraction pressure accentuated by the greater annual demand for firewood by the community, as well as to inefficient policing and management by forest owners (Bulafu et al., 2013; Baranga et al., 2009). We report AGB of between 21 t ha-1 and 83 t ha-1 and compared well with hardwood plantations in similar ecological zone, which can store between 88 ha-1 and 90 ha-1 (Drichi, 2003). Forest subjected to disturbance in the form of selective logging has been shown to have lower AGB than their potential (Brown, 1997). Disturbance and fragmentation both increase forest edge-related effects, consequently reducing forest capacity for AGB retention. Studies in fragmented Brazilian landscapes with high edge effects were shown to retain only one-third as much carbon as forest interior habitat (Dantas et al., 2011); the strength of fragmentation effects would probably vary with climate, and forest type.

In our study, the largest trees stored most (over 40%) of the AGB and carbon, underlining their importance. This agrees with other studies where large trees have been reported to account for more than 30% of AGB in mature forests (Brown and Lugo, 1992; Nascimento and Laurance, 2002). Private forest fragments had fewer large trees compared to the forest reserve and this is again related to anthropogenic disturbance (Bulafu et al., 2013). Over the re-sample period, our results show a reduction in the amount of AGB stored in some fragment, with high declines in basal area across size classes. These changes can be attributed to selective logging of trees and associated forest structural changes (Bulafu et al., 2013). In other studies, reduction in AGB and carbon retention have primarily been associated with increased mortality of large trees up to 300 m from forest edges (Chambers et al., 2001; Nascimento and Laurance, 2004; Alves et al., 2010) combined with a lack of compensatory effect of the remaining canopy and understorey (Dantas et al., 2011). For instance, AGB of forest edges in the Amazonian forest was reduced by one third in just 10-17 years after habitat fragmentation (Oliveira et al., 2008). A lesser contribution of large stems would also be expected for habitats that are more heavily logged such as most of our forest fragments (Chave et al., 2003; Baraloto et al., 2011). We document increases in AGB in the intermediate (20-40 cm DBH size class) in three forests in our study that showed marked declines in large sized trees and we interpreted this as a form of compensatory growth. This can be attributed to either recruitment of young trees into intermediate size classes being assisted by reduced competition from mature trees, or by limited or reduced mortality from human exploitation of intermediate size classes for timber or firewood. Pioneer species seemed to be responsible for this compensatory effect at least in two of the three forest fragments.

The increased mortality of large trees in some fragments may facilitate proliferation of long-lived pioneer species. The low value of mean wood density and subsequent per capita carbon relative to old-growth flora, suggest that increased long-lived pioneer species explain the low AGB and carbon retention in disturbed forests (Tabarelli et al., 2008). Rather than making only a minor contribution, Dantas et al., (2011) suggest that species replacement is a “key mechanism” in the recovery of biomass in stands where the large trees have been removed, such as the fragments in this study. Consequently marked variation in the AGB and species turnover of large trees have significant implications for carbon accounting and the future of tropical forests and calls for a better understanding of large tree allometry (Goodman et al., 2012). Belowground biomass was not measured in this study and estimates of it are scarce, it nevertheless represents an important stock of biomass. In tropical lowland terra firme rainforests in Brazilian Amazonia, belowground root biomass averaged 20% of AGB (Sarmiento et al., 2005).Using this mean value, root biomass in our forests would range from 5-12 t ha-1 across forest fragments in the current sample. We do not have an estimate of fine litter and coarse dead wood as their dynamics are poorly understood, although it has been estimated that coarse woody debris may be 10 to 40% of the AGB and can serve as a long term carbon pool. The amount given by Uhl and Kauffman (1990) here may be an overestimate for our forests as it is based on relatively intact forests.

For large well managed forests, the 2010 value of carbon revenues based on the carbon offset market wide average of $9.2 per tonne of sequestered carbon could present significant revenues gains based on present 2010 AGB. Africa saw 100% growth in contracted forest credit volumes, with 97%

of credits sold to voluntary buyers in the European Union. Uganda was the 4th largest offset supply country in 2011, mainly from REDD+ related projects (Peters-Stanley et al., 2012). The majority of projects are on private land but increasingly involve communities and smallholder landholders. However, transactional costs for small natural forest owners might be prohibitive to engage in improved forest management so as to benefit from the REDD+ carbon credits schemes compared to alternative agricultural land uses. In this case such forest stakeholders can be encouraged to avoid deforestation by the provision and support of alternative sources of income generation such as eco-tourism, non-timber forest products production and forest commodity processing. This would help compensate the full range of economic gains that would accrue from deforestation, i.e. the opportunity cost of abandoning less sustainable activities. When combined with restoration activities such forest could have the potential to increase their carbon value. Involvement of forest stakeholders in REDD+ carbon schemes is dependent mainly on involvement of private-sector institutions seeking to offset emissions to increase demand coupled with appropriate price signals (Peters-Stanley et al., 2012).

5. Conclusion

We show massive AGB variability between fragments over time. Our results confirm our prediction that differences in protection status will translate to noticeable differences in AGB loss that were driven mainly by forest structural changes. Further, there were differences between private and reserved forest tin term of which species constituted the greatest AGB. For instance, non-pioneer species constituted over 50% of AGB in reserve forest, in contrast to private forests where pioneer species dominated. Our study demonstrates the potential of private forests to hold comparable AGB to plantation. Reduction in exploitation pressure is required if fragments are to mitigate carbon emissions.

4.1. Implications for conservation

Despite a lower number of large trees in the private fragments compared to reserves and research forests, urban fringe fragments in the Kampala area store a considerable amount of carbon relative to plantation forests of similar size, mostly contained in large individuals that remained. Proper silvicultural management of these forest fragments, allowing more trees to gain large diameters, has the potential to increase mitigation of carbon emissions. Here we present more realistic estimates of the potential of poorly-managed or unprotected fragments to mitigate carbon emissions.

In our forests the greatest proportion of change in AGB was due to structural changes. At the current rate of AGB loss, some of the forest fragments are bound to lose even more of their stored above-ground carbon. The increased proliferation of pioneer species due to anthropogenic disturbances exacerbates this loss. If we are to promote forest fragments for carbon storage, exploitation should be reduced, especially for the large sized trees and late-successional species. However, exploitation is likely to increase in such small, edge-affected fragments as are found in human-modified landscapes such as the Kampala area. Owners of large and well managed forests fragments can earn money from carbon credit based on the carbon dioxide equivalent. Contracting them on the carbon markets will not only reduce carbon dioxide emissions but also present gains for biodiversity conservation, with associated reduction in poverty and improved livelihoods (Peters-Stanley *et al*., 2012). However, owners of smaller forests might be hampered due to high transactional costs and must engage in proper management practices and restoration activities, particularly for forest fragments that have been severely degraded, in order to benefit from REDD+ carbon credits schemes.

References

Alves, D.S., Soares, J.V., Amaral, S., Mello, E.M.K., Almeida, S.A.S., Silva, O.F., Silveira, A.M. 1997. Biomass of primary and secondary vegetation in Rondônia, Western Brazilian Amazon. *Global Change Biology* 3: 451–461.

Alves, L.F., Vieirac, S.A., Scaranelloc, M.A., Camargoc, P.B., Santosd, F.A.M., Joly, C.A., Martinelli, L.A. 2010. Forest structure and live above-ground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *Forest Ecology and Management* 260: 679–691.

Asner, G.P., Keller, M., Silva, J.N.M. 2004. Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. *Global Change Biology* 10**:** 765–783.

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Herault, B., Davila, N., Mesones, I., Rios, M., Valderrama, E., Fine, P.V.A. 2011. Disentangling stand and environmental correlates of above-ground biomass in Amazonian forests. *Global Change Biology* 17: 2677–2688.

Baranga, D. 2004. Forest fragmentation and primates' survival status in non-reserved forests of the 'Kampala area', Uganda. *African Journal of Ecology* 42: 70–77.

Baranga, D., Chapman, C.A., Kasenene, J.M. 2009. The structure and status of forest fragments outside protected areas in Central Uganda. *African Journal of Ecology* 47: 664–669.

Brown, S. 1997. *Estimating Biomass and Biomass Change of Tropical Forests: a Primer*. UN FAO Forestry Paper 134. Food and Agriculture Organisation, Rome.

Brown, S., Lugo, A.E. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian amazon. *Interciencia* 17: 8–18.

Bulafu, C., Baranga, D., Mucunguzi, P., Telford, R.J., Vandvik, V. 2013. Massive structural and compositional changes over two decades in forest fragments near Kampala, Uganda. *Ecology and Evolution, 3*, 3804–3823.

Chambers, J.Q., Santos, J., Ribeiro, R.J., Higuchi, N. 2001. Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecology and Management* 152: 73–84.

Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B., Hubbel, S.P. 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *Journal of Ecology* 191: 240–252.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Rie´ra, B., Yamakura, T. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Ter Steege, H., Webb, C.O. 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications* 16: 2356–2367.

Dantas de Paula, M., Alves-Costa, C.P., Tabarelli, M. 2011. Carbon storage in a fragmented landscape of Atlantic forest: the role played by edge-affected habitats and emergent trees. *Tropical Conservation Science* 4: 349–358.

Dawkins, H.C. and Philip, M.S. 1962. Working plan for Mpanga Research Forest. Uganda Forest Department.

Drichi, P. 2003. National biomass study. Technical report. Forest Department, Ministry of Water, Lands and Environment, Kampala, Uganda.

Eggeling, W.J. 1940. The indigenous trees of the Uganda protectorate. Government Printer, Entebbe, Uganda.

FAO 2006. Global forest resources assessment 2005: Progress towards sustainable forest management. FAO forestry paper. Rome, Food and Agricultural Organisation of the United Nations.

FRA 2010. Forest resources assessment. FAO, Forestry Paper 163, Roma.

Goodman, R.C., Phillip, O.L., Baker, T.R. 2012. Tropical forests: Tightening up on tree carbon estimates. *Nature* 491: 527.

Hamilton, A.C. 1981 *A Field Guide to Uganda Forest Trees.* Makerere University Printery, Kampala.

IPCC 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Vol. Geneva, p. 996, Cambridge University Press.

Langdale-Brown, I., Osmaston, H.A., Wilson, J.G. 1964. *The Vegetation of Uganda and its bearing to land-use*. Uganda Government Printer, Kampala.

Lwanga, J.S. 2003. Forest succession in Kibale National Park, Uganda: implications for forest restoration and management. *African Journal of Ecology* 41: 9–22.

MEA [Millennium Ecosystem Assessment]. 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*. Washington, DC, World Resources Institute, D.C.

Munishi, P.K.T. 2004. Carbon storage in afromontane rain forests of the Eastern Arc mountains of Tanzania: Their net contribution to atmospheric carbon. *Journal of Tropical Forest Science* 16: 78–93.

Naughton-Treves, L., Holland, M., Brandon, K. 2005. The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annual Review of Environment and Resources* 30: 219–252.

Nascimento, H.E.M. and Laurance, W.F. 2004. Biomass dynamics in Amazonian forest fragments. *Ecological Application*14 (suppl.):127–138.

Nascimento, H.E.M. and Laurance, W.F. 2002. Total above-ground biomass in central Amazonian rainforests: a landscape-scale study. *Forest Ecology and Management* 168: 311–321.

NEMA [National Environmental and Management Authority]. 2007. *State of Environment Report for Uganda*. NEMA. Kampala.

Oliveira, M.A., Santos, A.M.M., Tabarelli, M. 2008. Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. *Forest Ecology and Management* 256: 1910–1917.

Oliveira, M. A., Grillo, A.S., and Tabarelli, M. 2004. Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. Oryx 38: 389–394.

Peters-Stanley, M., Hamilton, K., Yin, D. 2012. Leveraging the landscape: State of the forest carbon markets. Ecosystem Marketplace. Available at http://www.forest-trends.org/documents/files/doc_3242.pdf (accessed 20 April 2013).

R Core Team 2013 *R:* A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at http://www.R-project.org/ (accessed 18 April 2013).Sarmiento, G., Pinillos, M., Garay, I. 2005. Biomass variability in tropical American lowland rainforests. *Ecotropicos* 18: 1–20.

Schleuning, M., Farwig, N., Peters, M.K., Bergsdorf, T., Bleher, B., Brandl, R., Dalitz, H., Fischer, G., Freund, W., Gikungu, M.W., Hagen, M., Garcia, F.H., Kagezi, G.H., Kaib, M., Kraemer, M., Lung, T., Naumann, C.M., Schaab, G., Templin, M., Uster, D., Wagele, J.W., Bahning-Gaese, K. 2011. Forest fragmentation and selective logging have inconsistent effects on multiple animal-mediated ecosystem processes in a tropical forest. *PLoS ONE,* 6(11) e27785. 10.1371/journal.pone.0027785 Sheil, D., Jennings, S., Savill, P. 2000. Long-term permanent plot observations of vegetation dynamics in Budongo, a Ugandan rain forest. *Journal of Tropical Ecology* 16: 865–882.

Tabarelli, M., Aguiar, A.V., Girao, L.C., Peres, C.A., Lopes, A.V. 2010. Effects of pioneer tree species hyperabundance on forest fragments in north-eastern Brazil. *Conservation Biology* 24: 1654–1663.

Tabarelli, M., Lopes, A.V., Peres, C.A. 2008. Edge-effects drive tropical forest fragments towards an early-successional system. *Biotropica* 40: 657–661.

Uhl, C. and Kauffman, J.B. (1990) Deforestation, fire susceptibility, and potential tree responses to fires in eastern Amazon. *Ecology* 71: 437–449.

Appendix 1: Summary of changes in forest fragments (government owned forests (A-C), privately owned forests (D-G church; H-J individual; k sacred) in Kampala area for the period 1990 to 2010. Forest areas and extent are based on 1955, 1995 and 2010 vegetation maps. Disturbance index: 1: fairly intact; 2: disturbed; 3: degraded; 4: highly degraded.

Forest name	**Code**	**GPS coordinates**	**No of transects**		**No. of plots**		**Forest size (ha)**		**Carbon**				**Disturbance index**	
			1990	2010	1990	2010	1995	2010	1990 (t ha^{-1})	1990 Total (Mt)	2010 (t ha^{-1})	2010 Total (Mt)	1990	2010
Mpanga	A	0°13'N, 32°18'E	5	5	50	48	476	438	50	23.8	46	20.15	1	1
Kituza	B	0°16'N, 32°47'E	5	5	48	49	98	110	34	3.33	42	4.51	1	1
Zika	C	0°07'N, 32°31'E	3	3	25	23	10	13	34	0.34	42	0.53	1	1
Kibale	D	0°07'N, 32°32'E	4	4	27	31	42	38	42	1.76	24	0.84	2	2
Kisubi Technical	E	0°07'N, 32°32'E	4	4	20	18	16	10	32	0.51	15	0.14	2	2
Gogonya	F	0°07'N, 32°32'E	4	4	21	21	15	11	48	0.72	11	0.12	2	3
Kisubi Girls	G	0°07'N, 32°32'E	5	5	47	18	15	13	28	0.42	14	0.18	3	3
Wamala	H	0°09'N, 32°31'E	6	6	31	30	19	19	45	0.86	29	0.55	2	2
Nzuki	I	0°09'N, 32°33'E	5	5	20	17	10	10	34	0.34	36	0.36	2	2
Bunamwaya	J	0°15'N, 32°33'E	7	7	26	23	9	9	38	0.34	32	0.28	3	2
Katwe	K	0°11'N, 32°27'E	4	4	42	18	18	5	37	0.67	39	0.19	2	2

Appendix 2: Aboveground Biomass (AGB t ha^{-1}) contribution by the five top tree species DBH ≥ 3.7 cm for forest fragments described in Appendix 1 for the two sample periods. See Appendix 1 for forest codes; A, B and C government owned whereas D-K are privately or community owned.

	Forests																					
Species	A		B		C		D		E		F		G		H		I		J		K	
	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010
Non pioneer species																						
Trilepisium madagascariense DC.*	**9.1**	**4.6**	**9.9**	**12.7**	**10.5**	**5.5**					**19.5**					**4.3**			4.1		**5.9**	**6.5**
Pseudospondias microcarpa (A.Rich.) Engl.*				**12.5**		**6.5**		**3.1**				**2.4**	4.0		68.6		**12.3**	**6.5**	17.4			
Antiaris toxicaria (Rumph.ex Pers.) Lesch.*				**7.4**		**3.9**						1.7			42.8		**4.1**	**4.3**		**6.6**	**5.0**	**5.8**
Manilkara butugi Chiov.*	**8.3**		6.0			**7.4**	**13.9**	**2.1**									6.6					
Sapium ellipticum (Hochst.ex Krauss) Pax*									10.5	5.8			14.4					**8.3**	**13.5**	**32.0**		
Vespris nobilis Engl.*							10.1		5.5								**10.4**	**3.8**		**5.5**		
Celtis durandii Engl.*	**14.4**	**7.3**	**5.7**	**5.2**																		
Tabernaemontana holstii K.Schum*			**7.5**	**5.3**						3.8					58.3							
Celtis mildbraedii Engl.*	**7.9**	**14.0**																				**7.0**

	Forests																					
Species	A		B		C		D		E		F		G		H		I		J		K	
	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010
Funtumia elastica (P.Preuss) Stapf*				**5.0**										**5.6**								
Syzygium guineense (Willd.) DC.*													2.8							**3.2**		
Blighia unijugata Bak.*																			**4.5**			
Trichilia prieuriana A.Juss.*	**11.4**	**6.0**																				
Manilkara dawei (Stapf) Chiov.*					8.8																	
Oxyanthus speciosus DC.*					3.8																	
Pioneer species																						
Maesopsis eminii Engl.						2.1		**6.5**	63.6	4.6	**10.4**	**4.4**		**8.3**		**4.1**		**4.2**		**5.4**		
Piptadeniastrum africanum (Hook.f.) Brenan					**4.4**	**4.7**				3.7	**13.4**	**5.9**									**19.7**	**25.2**
Erythrophleum suaveolens (Guill. & Perr.) Brenan					3.4	13.4	**6.0**	**5.1**								**4.4**						
Pycnanthus angolensis							5.7				**7.1**	**2.2**		**1.1**		**9.2**						

	Forests																					
Species	A		B		C		D		E		F		G		H		I		J		K	
	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010
(Welw.) Warb.																						
Artocarpus heterophyllus Lam.						0.7								**0.9**		**5.7**						
Lovoa trichilioides Harms						0.7															**5.9**	**8.0**
Musanga leo-errerae Hauman & j.Leonard															**20.9**	**4.8**	4.4					
Albizia zygia (DC.) Macbr.											8.9							**7.4**				
Canarium schweinfurthii Engl.						3.1								**1.9**								
Macaranga pynaertii De Wild.							6.8												**7.4**			
Bersama abyssinica Fres.													3.4									
Celtis zenkeri Engl.		**13.7**																				
Eucalyptus grandis W.Hill														**3.8**								
Milicia exelsa (Welw.) C.C.Berg								**3.4**														
Myrianthus holstii K.															5.9							

	Forests																					
Species	A		B		C		D		E		F		G		H		I		J		K	
	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010	1990	2010
Schum																						
Pinus patula Schltdl. & Cham.												**3.3**										
Psidium guajava L.													15.0									
Tetrorchidium didymostemon (Bail.) Pax & K. Hoffm.										2.5												
Theobroma cacao L.			15.1																			

. * *Non-pioneer species.*