

The role of remnant trees in carbon sequestration, vegetation structure and tree diversity of early succession regrowing fallows in eastern Sierra Leone

Aida Cuni Sanchez^{1,2*} and Jeremy A. Lindsell^{2,3}

¹Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark, ²The RSPB, The Lodge, Sandy, Bedfordshire, SG19 2DL, U.K. and ³A Rocha International, 3 Hooper St, Cambridge, CB1 2NZ, U.K.

Abstract

Remnant tree presence affects forest recovery after slash-and-burn agriculture. However, little is known about its effect on above-ground carbon stocks, especially in Africa. We focused our study on Sierra Leone, part of the Upper Guinean forests, an important centre of endemism threatened by encroachment and forest degradation. We studied 99 (20-m-radius) plots aged 2–10 years with and without remnant trees and compared their above-ground carbon stocks, vegetation structure (stem density, basal area) and tree diversity. Above-ground carbon stocks, stem density, basal area, species richness and tree diversity increased significantly with fallow age. Remnant tree presence affected significantly tree diversity, species dominance and above-ground carbon stocks, but not vegetation structure (stem density, basal area). Number of remnant trees and number of species of remnant trees were also important explanatory variables. Although other factors should be considered in future studies, such as the size and dispersal modes of remnant trees, our results highlight that more strategic inclusion of remnant trees is likely to favour carbon stock and forest recovery in old fallows. To our knowledge, this is the first study on early succession regrowing fallows in West Africa.

Key words: carbon, REDD, regrowth, remnant tree, slash-and-burn, tree diversity, Upper Guinean forests

Résumé

La présence d'arbres résiduels affecte le rétablissement d'une forêt après une période d'agriculture sur brûlis.

*Correspondence: E-mails: aidacuni@hotmail.com, aidacuni@snm.ku.dk

Pourtant, on sait peu de choses de leur effet sur les stocks de carbone en surface, spécialement en Afrique. Nous avons axé notre étude en Sierra Leone sur une partie des forêts de Haute Guinée, un centre important d'endémisme, menacé par les empiétements et la dégradation forestière. Nous avons étudié 99 parcelles (de 20m de rayon) âgées de deux à dix ans, avec ou sans arbres résiduels, et nous avons comparé leurs stocks de carbone en surface, la structure de la végétation (densité des troncs, surface terrière) et la diversité des arbres. Les stocks de carbone en surface, la densité des troncs, la surface terrière, la richesse en espèces et la diversité des arbres augmentaient significativement avec la durée de la jachère. La présence d'arbres résiduels affectait significativement la diversité des arbres, la dominance spécifique et les stocks de carbone en surface, mais pas la structure de la végétation (densité des troncs, surface terrière). Le nombre d'arbres restants et le nombre d'espèces parmi eux étaient aussi des variables importantes pouvant expliquer ces faits. Même s'il faudra tenir compte d'autres facteurs dans de nouvelles études, comme la taille et le mode de dispersion des arbres résiduels, nos résultats soulignent qu'une inclusion plus stratégique d'arbres résiduels est susceptible de favoriser le stockage du carbone et le rétablissement forestier dans d'anciennes jachères. À notre connaissance, ceci est la première étude des débuts de la repousse des jachères en Afrique de l'Ouest.

Introduction

Slash-and-burn agriculture, also referred to as shifting cultivation or swidden-fallow, is the most widely distributed form of agriculture in the tropics (Dalle & de Blois, 2006). In Africa only, 75% of primary forest loss and

degradation is attributed to it (Ickowitz, 2006). Slash-and-burn agriculture, which initially involves the cutting of forest followed by burning of the plant material, is practised for the production of annual food crops or perennial crops such as cocoa. As soils become depleted or weeds become more difficult to manage (Mertz *et al.*, 2008), farmers change fields over time, creating a mosaic landscape of fallows of variable ages (Forman, 1995).

About 40% of tropical secondary forest cover constitutes fallows at different stages of forest recovery (Blay, 2002). The timber and nontimber forest products (NTFP) from fallows are essential for the rural poor in the tropics (Corlett, 1995). Fallows also help maintain local biodiversity and generate ecosystem services such as carbon storage, protection of watersheds and prevention of soil erosion (Rerkasem *et al.*, 2009). As developing countries need to produce reliable information on carbon stocks for mechanisms such as REDD or REDD+ (see <http://redd.unfccc.int/>), there is a growing interest in understanding and quantifying carbon accumulation in fallows. Even in the Latin America context, where most carbon studies have taken place, this type of study is scarce (Fonseca, Benayas & Alice, 2011).

Forest regrowth and carbon accumulation in fallows is the consequence of complex interactions between biotic and abiotic factors (Chazdon, 2003). Apart from climate, soil type and altitude, tillage regime, fire intensity, selective cutting (protection of isolated trees), land-use history, distance to seed sources and the presence/absence of seed dispersing agents and seed predators are known to affect the species composition and structure of abandoned fallows (Carrière, Letourmy & McKey, 2002; Mwampambaa & Schwartz, 2011; Randriamalala *et al.*, 2012).

Precisely, how the protection of isolated trees (named remnant trees) during land clearing affects forest recovery is still not well understood. Remnant trees might favour the development of a 'nucleus of regeneration', by providing (i) feeding and/or perching sites for seed dispersers and thereby enhancing seed rain and/or (ii) favourable conditions of light, moisture and nutrients for establishment of forest trees (e.g. Viera, Uhl & Nepstad, 1994). While several studies have shown that species diversity is often greater in fallows having more remnant trees (e.g. Carrière, Letourmy & McKey, 2002), contradictory results have also been observed, and little attention has been paid to the role of remnant trees for above-ground carbon stocks (AGC).

To our knowledge, in Africa, fallows have mainly been studied in Madagascar (e.g. Randriamalala *et al.*, 2012,

2015), Cameroun (e.g. Njomgang *et al.*, 2011), Mozambique (Williams *et al.*, 2008), Zambia (Ando *et al.*, 2014) and Tanzania (Mwampambaa & Schwartz, 2011), with no information available for West African Upper Guinean forests. These forests are known to be one of the most important biodiversity hot spots and centres of biodiversity and endemism (Myers *et al.*, 2000). However, they are under pressure from degradation and conversion to agriculture (Mittermeier *et al.*, 2004), and many species in the region are now threatened with extinction as a result (IUCN, 2011).

Here, we quantify changing AGC, vegetation structure and tree diversity along a chronosequence of early succession abandoned fallows in eastern part of Sierra Leone, and how remnant tree presence affects this recovery. We focused on early succession fallows as these types of fallows are the more widespread in the landscape.

Materials and methods

Study area

This case study is located around Gola Rainforest National Park (GRNP) in eastern Sierra Leone (Fig. 1). The GRNP, located next to Liberia, is the largest remaining lowland moist evergreen high forest in Sierra Leone and lies at the western extremity of the Upper Guinea forest block. Annual rainfall is 2500–3000 mm, mostly falling in a single wet season from May to October. Communities in

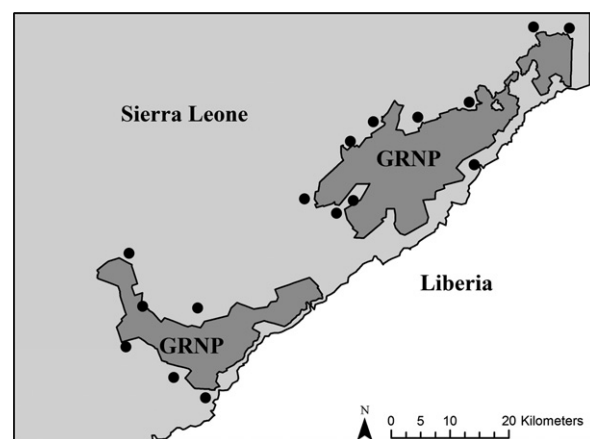


Fig 1 Selected villages (black dots) around the Gola Rainforest National Park (GRNP, dark grey colour) where fallows were sampled

the area are subsistence farmers, with few investing in cash crops such as cocoa and coffee. The traditional farming activities include inland valley swamp farming (mainly for rice) and upland farming (intercropping of rice, beans, maize, etc.). This study focuses on upland farming, which is based on slash-and burn agricultural practices. After tree felling and burning, farmers practise minimal tillage (using a hand plough) and sow their crops using basic tools. No manure or chemical fertilizer is used. Cleared fields are only cultivated for 1–2 years, due to low yields if longer cultivation is attempted. In the past, fallows would be cultivated again after >20 years, but due to population growth and land shortage in some villages, fallows are cultivated again after 7–10 years (Ministry of Transport and Aviation (MTA), 2007).

Sampling design and field measurements

Sixteen villages were randomly selected around GRNP (Fig. 1). At each village, six fallows of different ages identified through interviews with the farmers were surveyed. To sample a fallow of a given age, which usually extended <0.5 ha, a 20-m-radius circular plot was established at the approximate centre of the fallow. In total, 99 fallow plots were surveyed: 11 of each age ranging from 2 to 10 years. In each plot, all measurements followed a three-nest sampling plot methodology (Pearson, Brown & Birdsey, 2007); individual trees were measured for diameter (at breast height 1.3 m, DBH) and each tree was identified to species. Trees were measured according to subplot nest sizes: 4 m (trees ≥ 5 cm DBH), 14 m (trees ≥ 20 cm DBH) and 20 m (trees ≥ 50 cm DBH). DBH of trees with buttress was measured 30 cm above the buttress. For palms, only stem height was recorded, as height has been shown to be the best estimator for palm biomass (Gehring *et al.*, 2011).

Remnant trees (RT)

A tree found in a fallow was considered to be a 'remnant tree' depending upon farmer observations, species and tree size. As reported by local farmers, some fast-growing pioneer species are never left when land clearing. Trees which were not from these fast-growing pioneer species and which would have had an annual growth >3 cm year⁻¹ (considering fallow age) were considered to be remnant trees (thereafter named RT). We are aware that annual growth depends on species, climate, light and

soil conditions, among others (Gourlet-Fleury *et al.*, 2011). As annual growth of most trees found in this study was not available in the literature, following Gourlet-Fleury *et al.* (2011), Fayolle *et al.* (2012) and data from Fauset *et al.* (2012), the threshold of >3 cm year⁻¹ was selected. RT were not included in AGC, vegetation structure and tree diversity calculations of the plot concerned but were noted and used to create three explanatory variables: (a) RT tree presence/absence, (b) number of RT and (c) number of species of RT.

Above-ground carbon stocks (AGC)

At the individual tree level, the above-ground biomass (AGB) was estimated using the allometric equation of Chave *et al.* (2014) based on DBH + wood density + E (E is a measure of environmental stress) as total tree height was not measured in the field. The carbon fraction used to convert AGB to AGC was 0.47 (IPCC, 2006). Wood density was gathered from published databases (Chave *et al.*, 2009; Zanne *et al.*, 2009; Henry *et al.*, 2010). For palms, the biomass equation from Brown & Iverson (1992) was used. From the tree-level estimates, plots estimated were generated by scaling these to the unit of 1 ha, and as a function of the nested plot size. To compare our findings with regard to old fallows with those of other authors (see Discussion), the AGC of old fallows with RT (including the carbon of these RT) was also computed following the above-mentioned procedure.

Vegetation structure and tree diversity

For each plot, we calculated stem density and basal area (the sum of the cross-sectional area at 1.3 m, or above buttress, in m² ha⁻¹). Species richness was computed as total number of species observed in a given plot. The Shannon index (H') was also calculated. H' is a measure of biodiversity calculated from the relative abundance of species in community:

$$H' = \sum_{i=1}^S p_i \ln p_i$$

where $p_i = n_i/N$, n_i is the number of individuals present in species i , N is the total number of individuals, and S is the total number of species. Species dominance was calculated as: (i) dominant species in terms of total stem count (in percentage) and (ii) dominant species in terms of total

basal area (in percentage) for plots with and without remnant trees. In this case, fallows were grouped in 3 categories: young (2–3 years), medium (4–6 years) and old (7–10 years). This grouping reflects observed differences in vegetation structure: (a) young fallow: canopy cover <10%, vegetation height <2 m, bushblade (*Scleria boivinii*) and *Chromolaena* spp. common, which makes the field 'impenetrable'; (b) medium fallow: canopy cover >10%, tree height between 2 and 5 m, bushblade and *Chromolaena* spp. might be present but not common; and (c) old fallow: canopy cover >10%, tree height >5 m, no bushblade or *Chromolaena* spp.

Statistical analysis and limitations of our study

SPSS for Windows v 19.0 (IBM SPSS Statistics, Armonk, NY, USA), ANOVA and MANOVA were used to determine significant differences between fallow age and RT presence/absence, number of RT and number of species of RT. *Post hoc* pair wise multiple comparisons were performed using Tukey's *b*-test. Correlations were tested using Pearson correlation coefficient. Fallow age was kept as number of years (2–10 years) in the analysis of AGC, stem density, basal area, species richness and the Shannon index (H'). Fallows were grouped into 3 categories (young, medium, old) for the analysis of species dominance.

It should be noted that other variables such as RT height and canopy area are known to affect fallow recovery, but these could not be measured in the field. In a preliminary analysis, we explored the effects of RT diameter and

aggregate size of all RT. However, due to the large differences of DBH and aggregate sizes between plots with RT, these two explanatory variables did not have a significant effect in any variables studied (e.g. AGB, stem density). More plots should have been sampled to be able to quantify the effects of RT diameter and aggregate size of all RT.

Results

Above-ground carbon stocks

Above-ground carbon stocks increased significantly with fallow age ($P < 0.001$, Fig. 2). Neither RT presence nor the interaction between fallow age and RT presence had a significant effect on AGC, which increased at $4.9 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (Fig. 2). The number of RT and number of RT species did have a significant effect on AGC, with plots with more RT and/or more RT species having greater AGC (Fig. not included). It is interesting to notice that if RT would have been included in the AGC calculations, old fallows would have on average 80 Mg C ha^{-1} .

Vegetation structure

Stem density and basal area also increased significantly with fallow age ($P < 0.001$, Figs 3 and 4). In this case, RT presence, number of RT and number of RT species did not have a significant effect on neither stem density nor basal

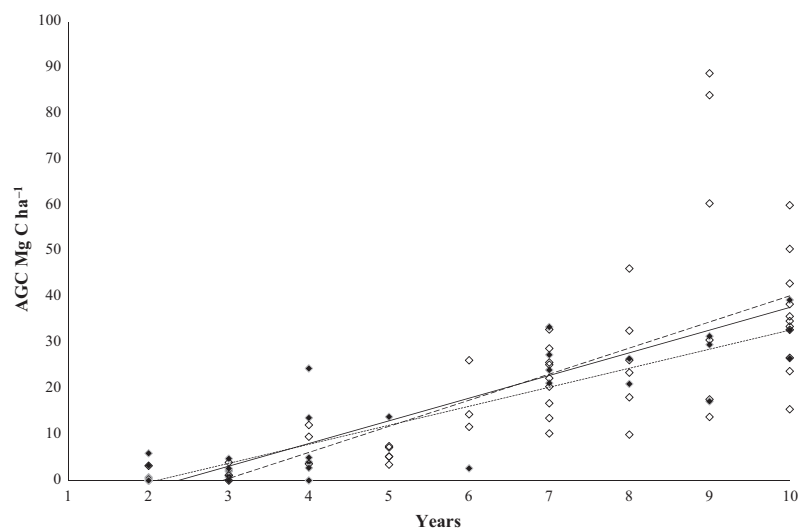


Fig 2 Above-ground carbon stocks (AGC) per plots plotted against fallow age (black squares = plots without remnant trees, white squares = plots with remnant trees), with a linear regression for all plots (black line), plots without remnant trees (short dash) and plots with remnant trees (long dash). Note that regressions are not significantly different. Regression parameters are $y = 4.9x - 11.7$ ($r^2 = 0.6$) for all plots

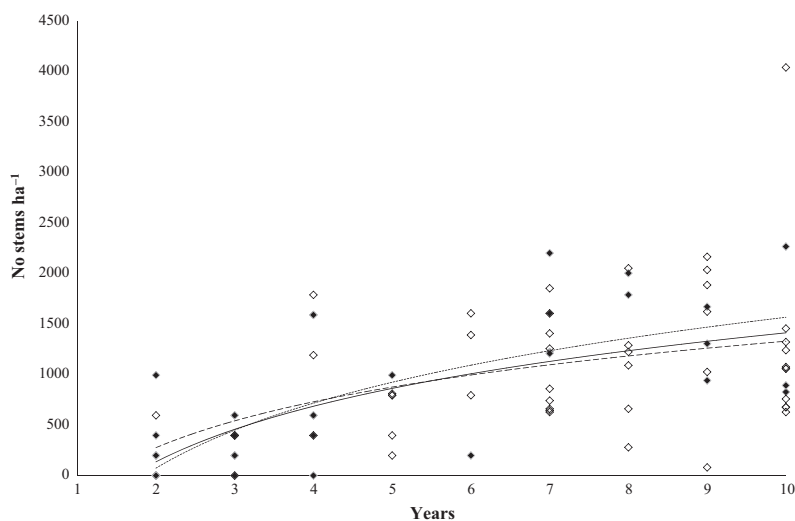


Fig 3 Measured stem density (stems per ha) plotted against fallow age (black squares = plots without remnant trees, white squares = plots with remnant trees), with nonlinear curve fit for all plots (black line), plots without remnant trees (short dash) and plots with remnant trees (long dash). Note that nonlinear curve fits are not significantly different. Parameters are $y = 793.8 \ln(x) - 413.9$ ($r^2 = 0.4$) for all plots

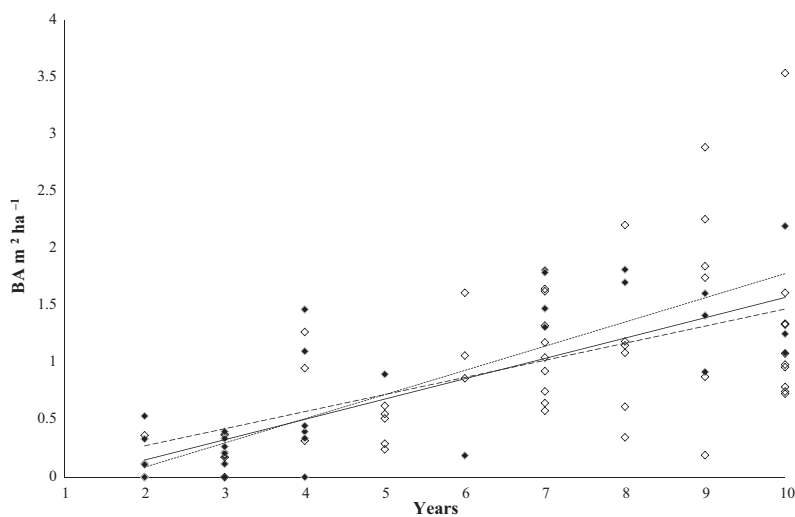


Fig 4 Measured basal area (BA) plotted against fallow age (black squares = plots without remnant trees, white squares = plots with remnant trees), with a linear regression for all plots (black line), plots without remnant trees (short dash) and plots with remnant trees (long dash). Note that regressions are not significantly different. Regression parameters are $y = 0.18x - 0.2$ ($r^2 = 0.5$) for all plots

area. While fallow age explained 40% of the observed variability in stem density, fallow age explained 50% of the variability in basal area (Figs 3 and 4). Basal area increment was $0.18 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$. Like for AGC, important differences between fallows of the same age group were observed for both basal area and stem density (Figs 3 and 4).

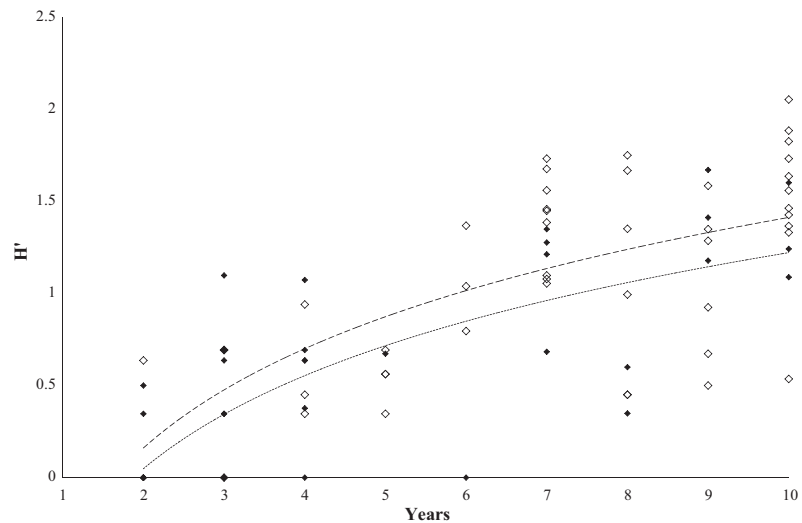
Tree diversity

Species richness and Shannon index also increased significantly with fallow age. The number of RT and the number of RT species had a significant effect on both species

richness and Shannon index, with plots with more RT and/or more RT species having greater species richness and Shannon index (Fig. not included). While fallow age explained 61% of the observed variability in Shannon index in fallows without RT, it only explained 36% in those with RT (Fig. 5), as number of RT and number of species of RT also played a role.

We identified 13, 24 and 27 species in young, medium and old fallows without RT, and 6, 26 and 64 species in young, medium and old fallows with RT (Table 1). The dominant species in fallows differed according to fallow age group and RT presence (Table 1). Two species (*Macaranga barteri* and *Margaritaria discoidea*) dominated in all cases. In

Fig 5 Shannon index (H') of species diversity plotted against fallow age (black squares = plots without remnant trees, white squares = plots with remnant trees), with nonlinear curve fit for plots without remnant trees (short dash) and plots with remnant trees (long dash). Parameters are $y = 0.72 \ln(x) - 0.45$ ($r^2 = 0.61$) for plots without remnant trees; and $y = 0.78 \ln(x) - 0.38$ ($r^2 = 0.36$) for plots with remnant trees. Note that nonlinear curve fits are significantly different at $P < 0.01$



fallows without RT, the three dominant species contributed to a greater percentage of the total stem count and basal area than in fallows with RT, as these later ones were more diverse (Table 1).

Discussion

This study assesses how AGC, vegetation structure and tree biodiversity recover in early succession abandoned fallows and how remnant tree presence affects this recovery. To our knowledge, this is the first of its kind not only in Sierra Leone but also in the Upper Guinean Forests' region.

Tree diversity

Species richness and Shannon indices increased with fallow age. Similar findings have been reported from fallows in Tanzania, Mozambique and Madagascar (Williams *et al.*, 2008; Mwampambaa & Schwartz, 2011; Randriamalala *et al.*, 2012). As expected, plots with more RT and/or more RT species had greater species richness and Shannon index, which has also been previously reported (e.g. Guevara *et al.*, 1992). RTs are visited by frugivorous vertebrates which feed and rest within their canopies. As a consequence, high-density clumps of seeds defecated or regurgitated by frugivores are typical under RTs. Beneath RTs, fluctuations in temperature and soil humidity are reduced, whereas soil fertility may be improved by decomposition of falling leaves and animal excretions (Viera, Uhl & Nepstad, 1994).

Fallows in Sierra Leone seem to have relatively high tree diversity. We identified 13, 24 and 27 tree species in young, medium and old fallows without RT, and 6, 26 and 64 tree species in those with RT. In southern Cameroun, 22 species were identified in 8- to 10-year fallows with RT, including herbs, lianas and woody species (Carrière, Letourmy & McKey, 2002). In eastern Madagascar, 18 and 41 species were found on 1- to 5-year and 6- to 10-year fallows, including herbs and woody species (Randriamalala *et al.*, 2012). It is possible that the short distance between fallows and old-growth forest edge in Sierra Leone explains this observation, although no specific information is available from the above-mentioned other studies.

In this study, dominant species in fallows differed according to fallow age and RT presence. Overall, ten species dominated: *Albizia adianthifolia*, *Albizia zygia*, *Dichrostachys cinerea*, *Funtumia africana*, *Macaranga barteri*, *Macaranga heudelotii*, *Margaritaria discoidea*, *Musanga cecropioides*, *Myrianthus serratus* and *Trema orientalis*; all of which are common medium-sized trees of secondary forests of West Africa (Hawthorne & Gyakari, 2006). While *Myrianthus serratus*, *Macaranga* spp., *Musanga cecropioides* and *Trema* spp. are considered rapidly growing pioneer species, *Funtumia* spp., and *Albizia* spp. are regarded as long-lived pioneer species. *Musanga* (like most rapidly growing pioneer species) does not grow under shade and thus, even if successfully dispersed to a fallow with an RT, may not grow well enough to outcompete other species. Considering that (i) *Musanga* was often amongst the dominant trees in fallows without RT but not in those with RT and (ii) *Funtumia africana* dominated in

Table 1 The most important dominant species ranked by stem density and basal area in each age class of abandoned fallow, percentage of contribution to total stem density and basal area; and total number of species recorded in age class

Order	Young fallow (1–3 years)		Medium fallow (4–6 years)		Old fallow (7–10 years)	
	RT absent	RT present	RT absent	RT present	RT absent	RT present
Dominance by stem density						
1	<i>Margaritaria discoidea</i> (Baill.) G.L.Webster	<i>Margaritaria discoidea</i> (Baill.) G.L.Webster	<i>Musanga cecropioides</i> R.Br. ex Teddie	<i>Macaranga barteri</i> Müll.Arg.	<i>Macaranga barteri</i> Müll.Arg.	<i>Funtumia africana</i> (Benth.) Stapf
2	<i>Trema orientalis</i> (L.) Blume		<i>Macaranga barteri</i> Müll.Arg.	<i>Myrianthus serratus</i> (Trécul) Benth.	<i>Musanga cecropioides</i> R.Br. ex Teddie	<i>Margaritaria discoidea</i> (Baill.) G.L.Webster
3	<i>Macaranga heudelotii</i> Baill.		<i>Albizia adianthifolia</i> (Schum.) W.Wight	<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	<i>Margaritaria discoidea</i> (Baill.) G.L.Webster	<i>Macaranga barteri</i> Müll.Arg.
% of total	52	25	56	35	71	41
No spp. recorded	13	6	24	26	27	64
Dominance by basal area						
1	<i>Margaritaria discoidea</i> (Baill.) G.L.Webster	<i>Margaritaria discoidea</i> (Baill.) G.L.Webster	<i>Musanga cecropioides</i> R.Br. ex Teddie	<i>Macaranga barteri</i> Müll.Arg.	<i>Macaranga barteri</i> Müll.Arg.	<i>Funtumia africana</i> (Benth.) Stapf
2	<i>Trema orientalis</i> (L.) Blume	<i>Macaranga heudelotii</i> Baill.	<i>Macaranga barteri</i> Müll.Arg.	<i>Musanga cecropioides</i> R.Br. ex Teddie	<i>Musanga cecropioides</i> R.Br. ex Teddie	<i>Margaritaria discoidea</i> (Baill.) G.L.Webster
3	<i>Macaranga heudelotii</i> Baill.	<i>Macaranga barteri</i> Müll.Arg.	<i>Albizia adianthifolia</i> (Schum.) W.Wight	<i>Myrianthus serratus</i> (Trécul) Benth.	<i>Albizia zygia</i> (DC.) J.F.Macbr.	<i>Macaranga barteri</i> Müll.Arg.
% of total	55	50	60	34	79	49

RT = remnant tree.

old fallows with RT, it seems that remnant tree presence generally short cut the first pioneer stage of *Musanga*. Similar results have been reported from southern Cameroun (Carrière, Letourmy & McKey, 2002).

Interestingly, some understorey trees of old-growth forests (*Diospyros cooperi*, *D. thomasi*) were observed in old fallows with RT, indicating that conditions had been favourable for their establishment (e.g. more shade). Although fallows in Sierra Leone have relatively high tree diversity (64 species in old fallows), the nearby old-growth forest has > 100 tree species (Klop, Lindsell & Siaka, 2008) and most dominant canopy species in GRNP were not observed in old fallows. The succession to old-growth forests is often long, from pioneer light demanders, to nonpioneer light demanders and finally shade-bearers.

Vegetation structure

Changes in vegetation structure were also observed with increasing fallow age. However, neither RT presence, nor number of RT nor RT species did have a significant effect on stem density or basal area. This is different from other studies which showed that woody stems were more numerous and stems were both larger and more variable in size beneath RT (Carrière, Letourmy & McKey, 2002). However, a recent study from Costa Rica also showed that RT did not locally affect stem density and basal area in old fallows (Sandor & Chazdon, 2014). It is also possible that in our study, high variation on basal area and stem density between fallows of similar age hampered the detection of any trends between RT presence/absence.

While fallows in Sierra Leone seem to be species' richer than others in Africa, their stem density and basal area appear lower. In this study, young, middle and old fallows had an average of 226, 850 and 1297 stems ha⁻¹ (respectively, see Fig. 3). In eastern Madagascar, 1- to 5-year and 6- to 10-year fallows had about 1000 and 17,000 stems ha⁻¹, respectively (Randriamalala *et al.*, 2012), which is higher than in our study. In our study, young, middle and old fallows had a basal area of 0.14, 0.69 and 1.34 m² ha⁻¹ (respectively, see Fig. 4), while in eastern Madagascar, 1- to 5-year and 6- to 10-year fallows had <1 and 13 m² ha⁻¹, respectively (Randriamalala *et al.*, 2012). In Tanzania, basal area was 6 and 9 m² ha⁻¹ for 5- and 10-year fallows, respectively (Mwampambaa & Schwartz, 2011).

Although basal area increased linearly with fallow age, stem density followed a logarithmic regression, with 7- to

10-year fallows having similar stem density. This latter observation indicates that self-thinning already started. In Mozambique, the self-thinning started between 15 and 20 years (Williams *et al.*, 2008). In our study area, as the canopy is already closed in 7-year fallows, the competition for resources (light) and therefore the self-thinning process might start earlier. Indeed, Carrière, Letourmy & McKey (2002) also pointed out at the high variability in basal area in 10-year fallows in southern Cameroun and suggested that this was a critical phase of competition that conditioned tree growth.

Above-ground carbon stocks

Above-ground carbon significantly increased with fallow age. While RT presence did not have a significant effect, number of RT and RT species did have a significant effect, with plots with more RT and/or more RT species having greater AGC. Our results suggest that it is the effect of RT on species diversity (wood density used for AGC calculations) that might affect AGC, rather than the effect of RT on stem density or basal area. Unfortunately, we could not find any reference quantifying the role of RT on fallow AGC recovery, and if its effect is related to species diversity, number of stems or higher growth rates.

Results indicate that fallows accumulated AGC at 4.9 Mg C ha⁻¹ year⁻¹. Higher rates have been reported from Cameroun (9.4 Mg C ha⁻¹ year⁻¹, Kotto-Same *et al.*, 1997), but in this later study, remnant tree growth was included in the figure. AGC of 10-year fallows in eastern Sierra Leone (about 40 Mg C ha⁻¹) are lower than values obtained for fallows in Central America: 82.2 Mg C ha⁻¹ have been reported in Costa Rica and 100 Mg C ha⁻¹ in Panama (Tschakert, Coomes & Potvin, 2007; Fonseca, Benayas & Alice, 2011), but these studies do not clarify if RT were included in the calculations.

Old fallows roughly had 25% of the mean value of 160 Mg C ha⁻¹ reported for GRNP (Lindsell & Klop, 2013). However, if RTs are included, old fallows have about 80 Mg C ha⁻¹, which is 50% of the value for GRNP. In Cameroun, forest fallows with RT had 50% carbon stocks of an old-growth forest (Njomgang *et al.*, 2011), while in Mozambique, 10-year fallows without RT had 50% carbon stocks of nearby woodland (Williams *et al.*, 2008). Several authors have shown that above-ground carbon recovery rates slow down after an initial face of fast recovery (e.g. Williams *et al.*, 2008; Martin, Newton & Bullock, 2013). Most likely, this is also the case in Sierra Leone.

Conclusions

We have shown that RT presence plays a considerable role in several aspects of forest regeneration in abandoned fallows. RT presence significantly affected tree biodiversity but not vegetation structure. The number of RT and RT species were also important explanatory variables as they affected AGC. Great variation within fallows of similar age having RT was observed. Future studies should also consider the size (e.g. diameter, crown size) and dispersal modes of RT. For example, Guevara *et al.* (1992) found that species richness of regrowth was higher beneath zoochorous RT than beneath those with other dispersal modes.

As suggested by other authors, more strategic inclusion of RT is likely to favour forest recovery in old fallows. However, as RTs compete with crops for nutrients, water and light, farmers are not willing to keep many RTs on their farms (Pers. Obs.). With current trends in population growth and increased demands of food, it does not seem likely that farmers will leave more RTs when land clearing. However, if there is an economic incentive (carbon projects, mechanisms such as REDD+), it could be possible.

Acknowledgements

This research was partially funded by RSPB. We acknowledge the people of Barrie, Gaura, Koya, Makpele, Malema, Nomo and Tunkia chiefdoms who gave us permission to work in their fallows and forest. We are grateful for the substantial contribution to fieldwork made by A. Jusu, M. Lumeh, M. Swaray, B.S. Turay and J.R. Kemp. We also express our gratitude to the kind support given by the team of GRNP and especially by A. Hillers and E. Tatum-Hume.

References

- ANDO, K., SHINJO, H., KURAMITSU, H., MIURA, R., SOKOTELA, S. & FUNAKAWA, S. (2014) Effects of cropping and short-natural fallow rotation on soil organic carbon in the Eastern Province of Zambia. *Agric. Ecosyst. Environ.* **196**, 34–41.
- BLAY, D. (2002) Tropical secondary forest management in humid Africa: reality and perspectives. FAO workshop on tropical secondary forest management in Africa: Nairobi, Kenya, 9–13 December 2002. Available at: <http://www.fao.org/docrep/006/j0628e/j0628e12.htm> (Accessed on 20 December 2015).
- BROWN, S. & IVERSON, L.R. (1992) Biomass estimates for tropical forests. *World Resour. Rev.* **4**, 366–383.
- CARRIÈRE, S.M., LETOURMY, P. & MCKEY, D.B. (2002) Effects of remnant trees in fallows on diversity and structure of forest regrowth in a slash-and-burn agricultural system in southern Cameroon. *J. Trop. Ecol.* **18**, 375–396.
- CHAVE, J., COOMES, D., JANSEN, S., LEWIS, S.L., SWENSON, N.G. & ZANNE, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecol. Lett.* **12**, 351–366.
- CHAVE, J., RÉJOU-MÉCHAIN, M., BÚRQUEZ, A., CHIDUMAYO, E., COLGAN, M.S., DELITTI, W.B.C., DUQUE, A., EID, T., FEARNSIDE, P.M., GOODMAN, R.C., HENRY, M., MARTÍNEZ-YRÍZAR, A., MUGASHA, W.A., MULLER-LANDAU, H.C., MENCUCINI, M., NELSON, B.W., NGOMANDA, A., NOGUEIRA, E.M., ORTIZ-MALAVASSI, E., PÉLISSIER, R., PLOTON, P., RYAN, C.M., SILDARRIAGA, J.G. & VIELLEDENT, G. (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Change Biol.* doi: 10.1111/gcb.12629
- CHAZDON, R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* **6**, 51–71.
- CORLETT, R.T. (1995) Tropical secondary forests. *Prog. Phys. Geog.* **19**, 159–172.
- DALLE, S.P. & DE BLOIS, S. (2006) Shorter fallow cycles affect the availability of non-crop plant resources in a shifting cultivation system. *Ecol. Soc.* **11**, 2.
- FAUSET, S., BAKER, T.R., LEWIS, S.L., FELDPAUSCH, T.R., AFFUM-BAFFOE, K., FOLI, E.G., HAMER, K.C. & SWAINE, M.D. (2012) Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecol. Lett.* **15**, 1120–1129.
- FAYOLLE, A., ENGELBRECHT, B., FREYCON, V., MORTIER, F. & SWAINE, M. (2012) Geological substrates shape tree species and trait distributions in African moist forests. *PLoS ONE* **7**, e42381.
- FONSECA, W., BENAYAS, J.M.R. & ALICE, F.E. (2011) Carbon accumulation in the biomass and soil of different aged secondary forests in the humid tropics of Costa Rica. *For. Ecol. Manage.* **262**, 1400–1408.
- FORMAN, R.T.T. (1995) *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge, UK.
- GEHRING, C., ZELARAYAN, M.L.C., ALMEIDA, R. & MORAES, F.H.R. (2011) Allometry of the babassu palm growing on slash-and-burn agroecosystem of the eastern periphery of Amazonia. *Acta Amazon* **41**, 127–134.
- GOURLET-FLEURY, S., ROSSI, V., REJOU-MÉCHAIN, M., FREYCON, V., FAYOLLE, A., SAINT-ANDRÉ, L., CORNU, G., GÉRARD, J., SARRAILH, J.-M., FLORES, O., BAYA, F., BILLAND, A., FAUVET, N., GALLY, M., HENRY, M., HUBERT, D., PASQUIER, A. & PICARD, N. (2011) Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests. *J. Ecol.* **99**, 981–990.
- GUEVARA, S., MEAVE, J., MORENO-CASASOLA, P. & LABORDE, J. (1992) Floristic composition and structure of vegetation under isolated trees in neotropical pastures. *J. Veg. Sci.* **3**, 655–664.
- HAWTHORNE, W.D. & GYAKARI, N. (2006) *Photoguide for the Forest Trees of Ghana. A Tree-spotter's Field Guide for Identifying the Largest Trees*. Oxford Forestry Institute, Oxford, UK.

- HENRY, M., BESNARD, A., ASANTE, W.A., ESHUN, J., ADU-BREDU, S., VALENTINI, R., BERNOUX, M. & SAINT-ANDRE, L. (2010) Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa. *For. Ecol. Manage.* **260**, 1375–1388.
- ICKOWITZ, A. (2006) Shifting cultivation and deforestation in tropical Africa: critical reflections. *Dev Change* **37**, 599–626.
- IPCC (2006) 2006 IPCC Guidelines for National Greenhouse Gas Inventories. (Ed. The National Greenhouse Gas Inventories Programme, H.S. EGGLESTON, L. BUENDIA, K. MIWA, T. NGARA and K. TANABE). IGES, Hayama, Japan.
- IUCN (2011) IUCN Red List of Threatened Species. Version 2011.1. IUCN, Gland, Available at: www.iucnredlist.org. (Accessed on 20 December 2015).
- KLOP, E., LINDSELL, J.A. & SIAKA, A. (2008) *Biodiversity of Gola Forest*. RSPB and CSSL, Sierra Leone.
- KOTTO-SAME, J., WOOMER, P.L., APPOLINAIRE, M. & LOUIS, Z. (1997) Carbon dynamics in slash-and-bum agriculture and land use alternatives of the humid forest zone in Cameroon. *Agric. Ecosyst. Environ.* **65**, 245–256.
- LINDSELL, J.A. & KLOP, E. (2013) Spatial and temporal variation of Carbon stocks in a lowland tropical forest in West Africa. *For. Ecol. Manage.* **289**, 10–17.
- MARTIN, P.A., NEWTON, A.C. & BULLOCK, J.M. (2013) Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proc. R. Soc. B* **280**, 20132236.
- MERTZ, O., WADLEY, R.L., NIELSEN, U., BRUUN, T.B., COLFER, C.J.P., DE NEERGAARD, A., JEPSEN, M.R., MARTINUSSEN, T., ZHAO NOWEG, G.T. & MAGID, J. (2008) A fresh look at shifting cultivation: fallow length an uncertain indicator of productivity. *Agricult. Syst.* **96**, 75–84.
- Ministry of Transport and Aviation (MTA) (2007) National Adaptation Programme of Action (NAPA). Final Report for UNDP, Government of Sierra Leone.
- MITTERMEIER, R.A., ROBLES GIL, P., HOFFMANN, M., PILGRIM, J., BROOKS, T., MITTERMEIER, C.G., LAMOREUX, J. & DA FONSECA, G.A.B. (2004) *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. University of Chicago Press, Mexico City, Mexico.
- MWAMPAMBAA, T.H. & SCHWARTZ, M.W. (2011) The effects of cultivation history on forest recovery in fallows in the Eastern Arc Mountain, Tanzania. *For. Ecol. Manage.* **261**, 1042–1052.
- MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., DA FONSECA, G.A.B. & KENT, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- NJOMGANG, R., YEMEFACK, M., NOUNAMO, L., MOUKAM, A. & KOTTO-SAME, J. (2011) Dynamics of shifting agricultural systems and organic Carbon sequestration in southern Cameroun. *Tropicultura* **29**, 176–182.
- PEARSON, T.R.H., BROWN, S.L. & BIRDSEY, R.A. (2007) Measurement guidelines for the sequestration of forest Carbon. General Technical Report NRS-18. US Department of Agriculture, Forest Service, Northern Research Station, Newton Square, Pennsylvania, US.
- RANDRIAMALALA, J.R., HERVÉ, D., RANDRIAMBOAVONJY, J.-C. & CARRIÈRE, S.M. (2012) Effects of tillage regime, cropping duration and fallow age on diversity and structure of secondary vegetation in Madagascar. *Agric. Ecosyst. Environ.* **155**, 182–193.
- RANDRIAMALALA, J.R., HERVÉ, D., LETOURMY, P. & CARRIÈRE, S.M. (2015) Effects of slash-and-burn practices on soil seed banks in secondary forest successions in Madagascar. *Agric. Ecosyst. Environ.* **199**, 312–319.
- REKASEM, K., LAWRENCE, D., PADOCH, C., SCHMIDT-VOGT, D., ZIEGLER, A.D. & BRUUN, T.B. (2009) Consequences of swidden transitions for crop and fallow biodiversity in Southeast Asia. *Hum. Ecol.* **37**, 347–360.
- SANDOR, M.E. & CHAZDON, R.L. (2014) Remnant trees affect species composition but not structure of tropical second-growth forest. *PLoS ONE* **9**, e83284.
- TSCHAKERT, P., COOMES, O.T. & POTVIN, C. (2007) Indigenous livelihoods, slash-and-burn agriculture and Carbon stocks in Eastern Panama. *Ecol. Econ.* **60**, 807–820.
- VIERA, I.C.G., UHL, C. & NEPSTAD, D. (1994) The role of the shrub *Cordia multispicata* Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazonia. *Vegetatio* **115**, 91–99.
- WILLIAMS, M., RYAN, C.M., REES, R.M., SAMBANE, E., FERNANDO, J. & GRACE, J. (2008) Carbon sequestration and biodiversity in re-growing miombo woodlands in Mozambique. *For. Ecol. Manage.* **254**, 145–155.
- ZANNE, A., LOPEZ-GONZALEZ, G., COOMES, D.A., ILIC, J., JANSEN, S., LEWIS, S.L., MILLER, R.B., SWENSON, N.G., WIEMANN, M.C. & CHAVE, J. (2009) Towards a Worldwide Wood Economics, Spectrum. *Ecol. Lett.* **12**, 351–366.

(Manuscript accepted 31 May 2016)

doi: 10.1111/aje.12340