QUANTIFYING BIOMASS OF SECONDARY FOREST AFTER SLASH-AND-BURN CULTIVATION IN CENTRAL MENABE, MADAGASCAR

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Received July 2011

RAHARIMALALA O, BUTTLER A, SCHLAEPFER R & GOBAT J-M. 2012. Quantifying biomass of secondary forest after slash-and-burn cultivation in Central Menabe, Madagascar. Biomass is the principal input of nutrients in slash-and-burn cultivation of tropical dry deciduous forest. In this paper, we report the aboveground biomass of ligneous and herbaceous vegetation as a function of the age of abandonment after cultivation in order to analyse the potential amount of nutrients released into the soil. To estimate the biomass of trees, we used dendrometric classes based on height and circumference at breast height of all individual plants inventoried in the plots in four growth types. For biomass measures, we harvested representative trees in each defined class. The quantity of total biomass increased with age of abandonment, reaching 72 t ha^{-1} after 40 years of abandonment. The species that contributed most to biomass were *Fernandoa madagascariensis, Diospyros perrieri, Dalbergia* sp., *Poupartia silvatica, Tarenna sericea, Xeromphis* sp., *Phylloctenium decaryanum, Stereospermum euphorioides* and *Croton greveanum*. *Diospyros* increased regularly already after 10 years of abandonment. The biomass of *Dalbergia* also increased with the age of abandonment, but after 30 years, this quantity decreased because of selective harvest by farmers. *Fernandoa* increased after 30 years, as did *Poupartia*, but the latter became a key player as it was, comparatively, the species with the highest biomass shortly after 30 years of abandonment.

Keywords: Fire, tropical dry forest, vegetation succession, agriculture, soil fertility, wood

RAHARIMALALA O, BUTTLER A, SCHLAEPFER R & GOBAT J-M. 2012. Penilaian biojisim hutan sekunder selepas pertanian tebang-bakar di Menabe Tengah, Madagascar. Biojisim merupakan input nutrien yang utama dalam pertanian tebang-bakar di hutan daun luruh tropika kering. Artikel ini melaporkan biojisim atas tanah vegetasi lignin dan herba mengikut tempoh peninggalan aktiviti pertanian. Kajian ini menilai potensi kandungan nutrien yang dilepaskan dalam tanah. Bagi menganggar biojisim pokok, kami menggunakan kelas dendrometrik ketinggian dan ukur lilit pada aras dada kesemua tumbuhan yang diinventori di dalam plot keempat-empat jenis pertumbuhan. Bagi penilaian biojisim, kami menebang sampel pokok daripada setiap kelas. Kuantiti jumlah biojisim bertambah dengan tempoh peninggalan dan mencapai 72 t ha^{-1} selepas 40 tahun peninggalan. Spesies yang paling banyak menyumbang kepada biojisim ialah *Fernandoa madagascariensis, Diospyros perrieri, Dalbergia* sp., *Poupartia silvatica, Tarenna sericea, Xeromphis* sp., *Phylloctenium decaryanum, Stereospermum euphorioides* dan *Croton greveanum*. Biojisim *Diospyros* bertambah dengan tetap selepas 10 tahun peninggalan. Biojisim *Dalbergia* juga bertambah dengan tempoh peninggalan. Namun selepas 30 tahun, kuantiti biojisimnya berkurang disebabkan penuaian memilih oleh petani. Biojisim *Fernandoa* dan *Poupartia* bertambah selepas 30 tahun tetapi *Poupartia* merupakan spesies utama kerana nilai biojisimnya adalah tertinggi sebaik sahaja 30 tahun peninggalan.

INTRODUCTION

Madagascar's forests are among the most biologically rich and unique ecosystems in the world but, despite long-standing concern about their destruction, estimates of past forest cover and deforestation have varied widely (Ganzhorn et al. 2001, Dufils 2003, Harper et al. 2007). A yearly forest loss of 0.70–1.1% is an accepted figure for the period 1990–2000, with a more

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recent decrease to 0.35–0.53% (USAID 2007). Slash-and-burn agriculture is the traditional and predominant landuse practice in all forested regions of Madagascar and its relevance in the context of forest preservation is significant. In Madagascar (Dirac Ramohavelo 2009) as well as in West and Central Africa (Lubini 2003), secondary successions resulting mainly from slash-and-burn cultivation are of economic interest because they provide resources such as firewood, food plants, pastures for cattle, caterpillars and medicinal plants. Moreover, several commercial timber species can be found in secondary forests. Cultivation is the principal activity of the villagers in Central Menabe (south-western coast of Madagascar) and the villagers themselves consider agriculture as their most important activity (Dirac-Ramohavelo 2009). Farmers cultivate products which growth depends on rainfall, e.g. maize, cassava and groundnuts which are the basis of the local commerce and are consumed, sold or exchanged (Dirac Ramohavelo 2009). According to modern law, all forests in Madagascar belong to the state. The cleared forests and fallows, which become secondary forests, are considered freehold and belong to those who cleared the land, according to common law (Réau 2003). Genini (1996) described how natural and secondary forests were cleared during the cold and dry season (June–September) with consecutive gathering of logs and branches in piles around larger trees. The wood is dried for several weeks and finally burnt at the end of the dry season (in October). Fire destroys practically all vegetation except for big baobabs and tall-crown trees. For two to three years, people plant maize on areas cleared this way and then cassava and groundnuts. This type of farming does not require any maintenance until harvesting. It benefits from fertilisation by the burnt vegetation and yields about two tonnes of maize per hectare. Only a small fraction of the dead unburnt wood is used for fencing or firewood, the majority is left to rot.

The maize production decreases by 80% after four years of culture on the same plot (Réau 2002). As a consequence, these plots are cultivated with cassava or groundnuts and then abandoned because of declining fertility but also because of the increasing need for weeding. Some farmers limit their cyclic activities to secondary surfaces, reusing plots of various ages of abandonment, but others extend part of their cultivation into the natural forest. Each family clears up to 2 ha per year (including natural and secondary forests) and the average cultivated surface is about 0.86 ha (Dirac Ramohavelo 2009). Fire is also applied on fallows between harvests and not only in forested vegetation. These slash-and-burn methods lead to significant losses of nutritive elements in the soil and change the floristic composition (Milleville et al. 2000). In eastern Madagascar, Pfund (2000) highlighted the importance of soil–vegetation patterns in slash- and-burn cultivation systems and found some correlations between nitrogen, phosphorus and potassium contained in soil and in vegetation. Generally, the less elements found in the soil, the higher their content in the vegetation. Furthermore, he found that the biomass produced by fallow land contributed significantly to soil fertility and was thus a determinant of the farming cycles. According to the age, nitrogen, phosphorus, potassium, calcium and magnesium in the aboveground living biomass increased linearly with the age of the fallow (Toky & Ramakrishan 1983). In the primary dry deciduous forest of south-western Madagascar, compositions and quantities of nutrients in biomass were determined to verify whether this dry forest had similar physiological characteristics as those of other dry ecosystems of the world (Raherison & Grouzis 2005) .

Our general aim was to study the amount of nutrients released into the soil after slashing and burning of the aboveground biomass. In a previous paper, Raharimalala et al. 2010 presented the soil vegetation patterns using basic soil properties and concluded that fields older than 20 years had recovered sufficiently to be reused as agricultural land. In this paper, we report the aboveground biomass of ligneous and herbaceous vegetation as a function of the age of abandonment (number of years after last cultivation) in order to analyse the potential amount of nutrients which could be made available for cultivation in secondary vegetation. The different questions studied are:

(1) How is biomass of herbaceous and ligneous vegetation related to the age of abandonment?
(2) How is the biomass of dominant species related to the age of abandonment?
(3) How are the different tree parts (stems, branches, leaves) contributing to the biomass?

(4) Can we validate the biomass obtained indirectly from biometric measurements and selective sampling for biomass weighting with the measure of the total biomass after clear cut?

MATERIALS AND METHODS

Study site

The study site (about 1000 ha) is located in Andranolava near Beroboka (19° 58' S – 44° 36' E) in south-western Madagascar, 75 km north of Morondava (Central Menabe), near the well-known Kirindy forest (Sorg et al. 2003) and the village of Berobouka. In the northern part, the area is characterised by old sisal plantations, the southern part is delimited by the Andranolava river, eastern part by the Kirindy forest and western part by littoral forest.

The climate of Central Menabe is classified as tropical dry with two distinct seasons: a rainy season (November till March) and a dry season (April till October) (Sorg & Rohner 1996). Data from the meteorological office (2000–2006) (Rakotondrabe 2007) show that the average annual temperature is 26 °C, with a relatively cool period from June till August. Average total precipitation is 791 mm per year. The study area can be classified as tropical dry forest (Murphy & Lugo 1986a). Vegetation is dominated by dry deciduous forests of various types as described in Koechlin et al. (1997).

Red and yellow soils were classified by Felber (1984) and Rohner and Sorg (1986) as 'red and yellow soils of the luvisols ferric' category, and could be named according to the French classification 'ferruginous tropical leached soils' (Rakotovao et al. 1988). For this study the yellow soils were chosen. They are preferred by farmers for cultivation (Raharimalala et al. 2010).

Plot selection

We selected 30 plots across six age classes on yellow soils according to the age of abandonment. These plots were chosen in homogenous vegetation patches (see also Raharimalala et al. 2010). Each class of age had five replicated plots taken randomly across the entire area of study. Age classes of 1 to 5 years and 6 to 10 years were surveyed on plots of 16 m^2, age classes of 11 to 20 years and of 21 to 30 years on plots of 64 m^2, and age classes of 31 to 40 years and more than 40 years on plots of 256 m^2. The surveyed surface was taken according to the minimal area rule (Barkman 1989) and thus depended on the vegetation structure (see Raharimalala et al. 2010). The age of the abandoned surface was estimated by a local guide who had already worked with many scientists in the area and was a former guide in the Kirindy forest. This information was cross-checked by consulting local farmers who visited the field with us when plots were selected.

Biometric measures on trees and tree selection for biomass measurements

We numbered all individual trees having reached breast height and wood climbers in the plot. We measured circumference at breast height according to Hashimoto et al. (2004) and Kale et al. (2004) and visually estimated the height after training with a clinometer on isolated trees. We separated four growth types: single-stemmed, with fork on the trunk, with fork from the base which could be considered multi-stemmed and small bush which was similar to plant with fork from the base but had a height smaller than 1.3 m (Figure 1). The latter comprised true bushes and young sprouting trees that would ultimately become multi-stemmed. Each individual was registered by a unique identification number, with its species name, its growth type as well as the plot number and the age of abandonment.

For fresh biomass measurement, the aim was to select some trees in order to have a representative sample. Whenever possible, we tried to have, for each species, individuals in all represented growth types, and in all represented class of abandonment. Nevertheless, our sample remained unbalanced for growth types and classes of age of abandonment. For all recorded species in all four growth types and all five classes of age of abandonment (class I was not used since plots were treeless), we ranked the individual trees according to the calculated variable circumference × height. For the growth types 'with fork on the trunk' or 'with fork from the base (multi-stemmed)', we took as circumference the sum of the circumferences of each fork. For growth type 'small bush', we ranked the individuals only according to the height. We then defined a certain number of classes and took, for biomass harvest and measurements, an individual tree in the median of each class (see example in Figure 2).

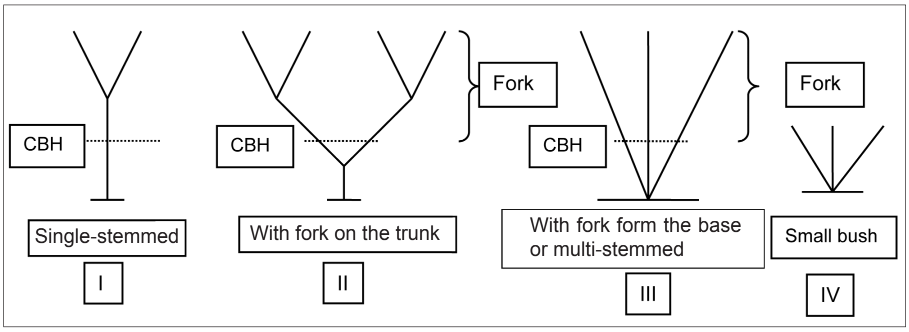

Figure 1 Growth types (I, II, III, IV) considered for biometric measurements; CBH = circumference at breast height (1.3 m)

The sampling effort in the different categories for biomass measurement can be seen in Table 1. For a total of 433 trees representing 61 species, there were 100 individuals in growth type I, 41 in growth type II, 208 in growth type III and 84 in growth type IV.

The selected trees were cut at ground level. The aboveground fresh biomass was weighed separately for branches, which were piled according to three size classes (small, median or large), leaves and stems. When there were several branches in each branch class, we weighed one branch which we considered as average, as well as leaves from this branch, and multiplied their weight by the number of branches. This was done for the three classes of branches and, adding the three values, this gave the total fresh weight of branches and leaves. We used two types of scales: one for leaves and small branches with a precision of 0.01 g, and one for stems and large branches with a precision of 0.050 kg.

Biomass of herbaceous vegetation and litter

Depending on spatial pattern of the herbaceous vegetation, we sampled subplots in two different manners. When the green biomass and litter were covering the ground homogeneously, we took randomly one square of 2 m × 2 m. We cut all herbaceous vegetation at the ground level and weighed its biomass. The litter was weighed separately. All measures were taken with a precision of 0.01 g and expressed as kg ha^{-1} of fresh weight. When there was a clear ground cover heterogeneity, we sampled according to two strata: one subplot of 2 m × 2 m was taken in the surface where green herbaceous vegetation was dominating and another subplot was taken where the litter was dominant. We then weighed the biomass and litter according to the proportion occupied by each strata in the plot so as to have an average biomass and litter value per plot, again expressed as kg ha^{-1} of fresh weight.

Dry biomass estimation

Our assumption was that, for a given tree species, the relative water loss during the drying process was the same irrespective of size, growth type and age of abandonment. We selected 28 tree species with a total frequency in the inventory of all plots higher than four individuals, without considering those present only as growth type IV (see Appendix 1). For each species, we selected three trees (replications) from the plot with the highest numbers of trees of the considered species. Whenever possible we took these three trees from growth type I (single-stemmed), otherwise we took those from growth types II, III or IV. At the end of the dry season, we cut each tree and from these 84 individuals we selected five morphological parts: part 1 corresponded to a piece of wood (roughly 400 g) at the bottom of the stem, part 2 to the top of the stem, part 3 to a piece of wood (roughly 100 g) at the bottom of an average fork, part 4 to the top of an average fork (roughly 50–100 g) and part 5 to the leaves stripped from the branch taken in part 4. When growth types III or IV had to be used, we got only parts 3, 4 and 5. For the other species (32), we applied the mean values obtained for each part of these 28 species.

The five parts of the trees were weighed fresh, then again after air drying for 45 days (ADW) and drying in the oven for 30 days at 60 °C (ODW) for woody parts; these durations corresponding to the time needed to reach constant weight. This oven temperature was chosen because samples were further used for chemical content. For each

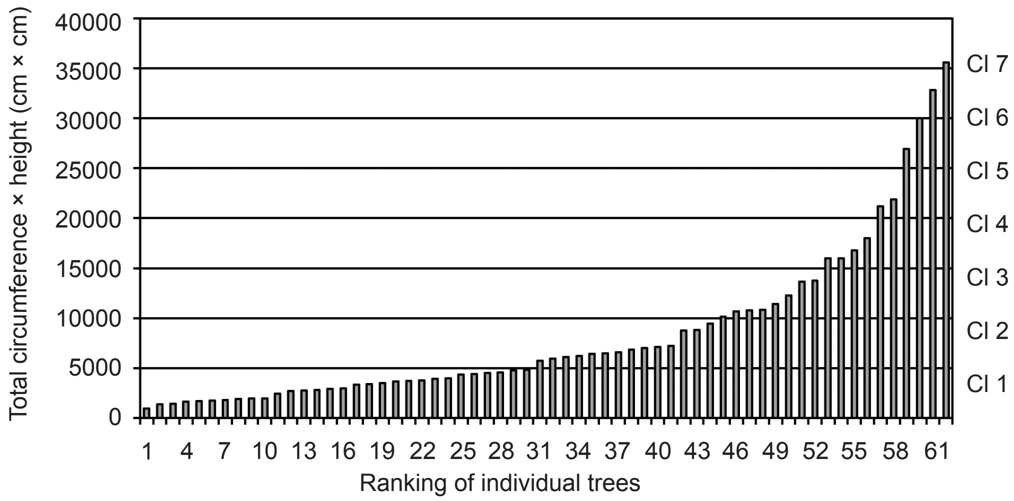

Figure 2 Example of class determination for *Diospyros perrieri* in the growth form with fork from the base (multi-stemmed) and age class of 31 to 40 years; individual trees were ranked according to the variable total circumference at breast height × height (cm × cm); seven classes of 'total circumference × height' (Cl 1 to 7) were defined: < 5000; 5000–10,000; 10,000–15,000; 15,000–20,000; 20,000–25,000; 25,000–30,000; > 30,000; we took the median individual of each class for harvesting and measuring its biomass

Table 1 Sampling effort (numbers of measured trees) for tree biomass estimation according to the age of abandonment and growth type

Age of abandonment	Growth type				Total
(years)	I	II	III	IV	
1–5	0	0	0	2	2
6–10	0	0	1	5	6
11–20	7	0	5	14	26
21–30	31	8	25	16	80
31–40	28	16	83	23	150
More than 40	34	17	94	24	169
Total	100	41	208	84	433

part, the water loss was obtained and expressed as per cent of the fresh weight. The relative water loss of the stem was calculated as the average of the relative water loss of parts 1, 2 and 3 (bottom of stem, top of stem and bottom of the fork). The relative water loss for branches resulted from part 4 and the one for leaves from part 5. We obtained the dry biomass of the trunk, the branches and the leaves of each tree by multiplying the fresh biomass by their respective relative dry matter content, calculated as 100% minus the relative water loss.

For the dry biomass of herbaceous vegetation, we took in each 2 m × 2 m subplot one bunch of vegetation. We measured its fresh biomass and air dried it for three weeks, which was enough to reach a constant weight. We obtained the dry biomass of the herbaceous layer by multiplying the fresh biomass by its respective relative dry matter content, calculated as 100% minus the relative water loss.

Total biomass at plot scale

For the ligneous vegetation, we identified the class (circumference × height) of each individual tree in the plot and attributed to it the biomass of the corresponding cut and measured tree with respect to species, growth type and age class. The total biomass of each plot was obtained by adding the biomass values of ligneous vegetation (growth types I to IV), of herbaceous vegetation and of litter. All dead branches lying on the soil in the plots were identified and weighed. They were added to the quantity of dry biomass of branches. Finally the result for each plot was presented as fresh and dry (air and oven) biomass of stems, branches, leaves and herbaceous vegetation, as well as the total fresh and dry biomass.

Bulk biomass

In order to validate the biomass values obtained with the above described biometric method, we chose one plot within each class of abandonment, based on the vegetation surveys (Raharimalala et al. 2010). We cut every tree and air dried the wood during one month on the soil, similarly to the common practice among farmers at the end of the dry season. We then weighed all the wood. The herbaceous vegetation and the litter were collected in five 1-m^2 subplots. This allowed us to calculate the bulk biomass of these plots.

RESULTS

Species richness and stand structure

Overall, 1101 individual trees and lianas were measured in 30 plots (total surveyed surface of 3360 m^2) (Appendix 1). They belonged to 27 families, 57 scientifically known and 3 species only known by their vernacular names. Among these species, we had plants with edible tubers, e.g. *Dioscorea acuminata*, plants with edible fruits or seeds, e.g. *Ziziphus mauritiana, Tamarindus indica* and *Phylloctenium decaryanum*, medicinal plants, e.g. *Fernandoa madagascariensis* and *Cryptostegia grandiflora*, and plants with economic uses such as *Jatropha curcas*, and especially *Dalbergia* sp. and *Diospyros perrieri*, which were used for their wood quality.

Appendix 1 shows that two species (*Tarenna sericea, Z. mauriatiana*) are observed in plots of 1 to 5 years of abandonment, four (*Dalbergia* sp. *Mussaenda arcuata, Stereospermum euphorioides, Albizia bernieri*) of 6 to 10 years, 10 (e.g. *F. madagascariensis, D. perrieri, Poupartia silvatica, P. decaryanum*) of 11 to 20 years, 18 (e.g. *Apaloxylon tuberosum, Ripikala, Grewia* sp. *Strychnos decussata, Xeromphis* sp. *Brachylaena microphylla*) of 21 to 30 years, 20 (e.g. *Isolona madagascariensis*) of 31 to 40 years and six (e.g. *Croton greveanum, Clerodendron* sp.) after 40 years of abandonment. Twenty-three species (e.g. *Diospyros, Acalypha diminuata, Poupartia*) had the highest frequency in the class of abandonment of 31 to 40 years, 15 (e.g. *Fernandoa, Croton, Xeromphis*) in the class over 40 years, 17 (e.g. *Dalbergia, Tarenna, Mussaenda, Apaloxylon*) in the class of 21 to 30 years and five in the class of 11 to 20 years (*Ziziphus*, which was not observed after 30 years and *Phylloctenium*). Only one species (*Albizia*) had its maximum in the class of 6 to 10 years and none in the class of 1 to 5 years.

Appendix 1 and Table 1 show that during the first 5 years, only two species (*Ziziphus* and *Tarenna)* are observed as small bushes (growth type IV). After five years, single-stemmed (type I) and multi-stemmed plants (type III) appeared (e.g. *Ziziphus),* some additional bushes grew (e.g. *Dalbergia, Tarenna, Stereospermum* and *Albizia)* and some lianas (e.g. *Mussaenda)* were observed. Trees with fork on the trunk (type II) appeared only after 20 years. Their density was the highest in the class of 21 to 30 years and decreased after 30 years. The density of inventoried trees, lianas and bushes was the most important in the age class of 21 to 30, except for growth type III, which had the highest density in the class of 31 to 40 years (Table 2). Several species had high density and their maximum by about 30 years or soon after (e.g. *Fernandoa, Diospyros, Acalypha, Dalbergia, Poupartia, Tarenna, Mussaenda* and *Apoxylon)*. Some dominant species such as *Fernandoa* increased their density with age of abandonment, whereas some others such as *Dalbergia* and *Diospyros* decreased it after 30 or 40 years.

The mean circumference at breast height (CBH) and the mean height (H) in any growth type increased generally with the age of abandonment (Table 3), e.g. the mean circumference of breast height for the single-stemmed varied from 2.2 ± 0.2 cm in the class of 11 to 20 years to 9.6 ± 0.9 cm after 40 years, and the height varied from 169 ± 17 cm in the class of 11 to 20 years to 328 ± 14 cm after 40 years.

With respect to herbaceous plants, 40 species (26 scientifically known and 14 species known by their vernacular names) in 20 families were found in our study area (Appendix 2). The total number of species present in one age class varied between 15 and 18. A maximum of 18 species were observed between 11 and 30 years, but we noted a slight decrease in older plots. Three species were present in all age classes *(Commiphora lamii*, kidranta and mamaky hoho*)*.

Table 2 Density values of the inventoried trees and bushes as function of the age of abandonment and growth types (number of individuals per ha)

Age of abandonment (years)	Growth type I	II	III	IV	Total
1–5	0	0	0	250	250
6–10	125	0	250	750	1125
11–20	1063	0	344	1156	2563
21–30	2563	281	1281	1156	5281
31–40	742	188	1836	742	3508
More than 40	766	188	1430	664	3048

I, II, III and IV are growth types

Table 3 Means of circumference at breast height (CBH) and height (H) with standard errors of the inventoried trees as function of age of abandonment and growth type in 30 plots

Age of abandonment (years)	Growth type							
	I		II		III		IV	
	Mean CBH (cm)	Mean H (cm)	Mean CBH (cm)	Mean H (cm)	Mean CBH (cm)	Mean H (cm)	Mean CBH (cm)	Mean H (cm)
1–5	–	–	–	–	–	–	–	65 ± 15 (n = 2)
6–10	5.0 (n = 1)	190 (n = 1)	–	–	21.2 ± 9 (n = 2)	200 ± 25 (n = 2)	–	177 ± 30 (n = 6)
11–20	2.2 ± 0.2 (n = 34)	169 ± 17 (n = 34)	–	–	15.4 ± 2.6 (n = 11)	199 ± 9 (n = 11)	–	153 ± 11 (n = 37)
21–30	3.6 ± 0.5 (n = 81)	206 ± 14 (n = 81)	14.8 ± 2.5 (n = 9)	294 ± 22 (n = 9)	44.8 ± 6.7 (n = 41)	171 ± 14 (n = 41)	–	219 ± 17 (n = 38)
31–40	8.5 ± 0.9 (n = 95)	260 ± 11 (n = 95)	60.3 ± 8.9 (n = 24)	537 ± 59 (n = 24)	39.3 ± 3.0 (n = 224)	316 ± 7 (n = 224)	–	191 ± 12 (n = 106)
More than 40	9.6 ± 0.9 (n = 98)	328 ± 14 (n = 98)	101 ± 21 (n = 24)	562 ± 33 (n = 24)	65.0 ± 4.0 (n = 183)	418 ± 10 (n = 183)	–	242 ± 18 (n = 85)

I, II, III and IV are growth types; the numbers of individuals are given in parentheses; – indicates no value

Plant biomass

Herbaceous biomass decreased with age of abandonment, after having reached a maximum in the age class of 6 to10 years (Table 4). The tendency for litter biomass to increase was the inverse of herbaceous biomass, increasing over time to reach 3.5 ± 1.1 t ha^{-1} oven-dry biomass in the age class beyond 40 years. However, taken together herbaceous biomass and litter were highest in the early stage (6 to 10 years). For trees and lianas, the biomass increased with age of abandonment (Table 4).

The water loss during the drying process was highest for the branches, ranging from 58.7 to 63% in the different age classes, and lower for leaves (54.1 to 58.2%) and stems (38.5 to 44%).

The distribution of dry biomass in trees showed that, irrespective of the age class, more than half of the biomass was in stems (Table 5). The youngest stage (1–5 years) had proportionally much of its biomass in stems and leaves. With age of abandonment, the relative contribution of stems increased again, whereas those of leaves decreased.

The species that contributed most to biomass (more than 1 t ha^{-1} in any one of the age classes) are represented in Figure 3. *Diospyros perrieri* increased regularly after 10 years of abandonment. The biomass of *Dalbergia* sp.

Table 4 Means of fresh biomass (FB) and oven-dry biomass (ODB) (t ha^{-1}) of trees, lianas and herbaceous vegetation and litter per age of abandonment with standard errors (n = 5 plots per age of abandonment)

Age of abandonment (years)	Tree + liana		Herb		Litter		Tree + liana + herb + litter	
	FB	ODB	FB	ODB	FB	ODB	FB	ODB
1–5	0.79 ± 0.78	0.403 ± 0.401	4.4 ± 1.0	2.0 ± 0.5	1.0 ± 0.5	0.4 ± 0.2	6.19 ± 1.35	2.8 ± 0.7
5–10	2.3 ± 1.3	1.2 ± 0.7	5.3 ± 0.4	2.4 ± 0.2	3.2 ± 1.1	1.5 ± 0.5	10.8 ± 1.7	6.1 ± 0.9
11–20	5.5 ± 0.7	2.5 ± 0.3	4.8 ± 1.8	2.1 ± 0.8	4.1 ± 1.2	1.9 ± 0.5	14.4 ± 2.3	6.5 ± 0.9
21–30	35.3 ± 9.5	17.4 ± 4.2	2.5 ± 0.5	1.2 ± 0.2	4.5 ± 1.3	2.0 ± 0.6	42.3 ± 9.6	20.6 ± 4.2
31–40	78.7 ± 15.8	41.1 ± 8.4	2.1 ± 0.5	1.0 ± 0.2	4.4 ± 1.1	2.0 ± 0.5	85.2 ± 15.8	44.1 ± 8.4
More than 40 years	128.8 ± 23.0	66.9 ± 9.5	2.7 ± 0.6	1.2 ± 0.3	7.8 ± 1.0	3.5 ± 0.5	139.3 ± 24.0	71.6 ± 9.5

Values for oven-dry herbaceous vegetation and litter were taken over from air-dry values because the drying process was already reached with the air drying

Table 5 Distribution of dry biomass (oven-dry biomass, ODB) between stems, branches and leaves, as function of age of abandonment

Age of abandonment (years)	Stem		Branch		Leaf		Total
	t ha^{-1}	%	t ha^{-1}	%	t ha^{-1}	%	t ha^{-1}
1–5	0.26	65	0.081	20	0.059	15	0.4
6–10	0.79	66	0.3	25	0.11	9	1.19
11–20	1.18	48	0.95	38	0.36	14	2.49
21–30	11.02	63	4.98	29	1.38	8	17.38
31–40	27.01	66	11.3	27	2.79	7	41.1
More than 40 years	48.4	72	15.68	23	2.86	4	66.94

increased also with the age of abandonment, but after 30 years, this quantity decreased. *Fernandoa madagascariensis* increased its biomaas after 30 years. Other major biomass contributors were *P. sylvatica*, which increased drastically after 30 years, and *T. sericea*. *Croton greveanum* was a late arrival species that contributed importantly to biomass in the oldest age class.

DISCUSSION

Regeneration and tree growth types

Regeneration is an important process for forest sustainability and restoration. In exploited forests, regeneration can be achieved by planting, or naturally by sprouting or seed dispersal. Sprouting is the consequence of felling trees and leads to the multi-stemmed growth type, and indeed, in our study area, it is the most common growth type after 30 years. The high frequency of both multi-stemmed plants and small bushes is typical of exploited forests. Sprouting ability is more common and more important as a mechanism of regeneration in dry tropical forest than in rainforests (Murphy & Lugo 1986b, Kennard et al. 2002, McLaren & McDonald 2003, Vieira & Scariot 2006). The growth types, plants with single stems and forks on the trunks, appear as a sign of another form of regeneration using seed.

Resprouting after disturbances such as slash and burn is a shortcut for forest recovery because it bypasses the most vulnerable life stages and the new plants start with vigorous shoots (Bond & Midgley 2001, Kennard et al. 2002). However, species can lose their resprouting ability after sequential cutting, burning as well as a consequence of intensive tractor use (Uhl et al. 1988, de Rouw 1993, Sampaio & Salcedo 1993, Nepstad et al. 1996).

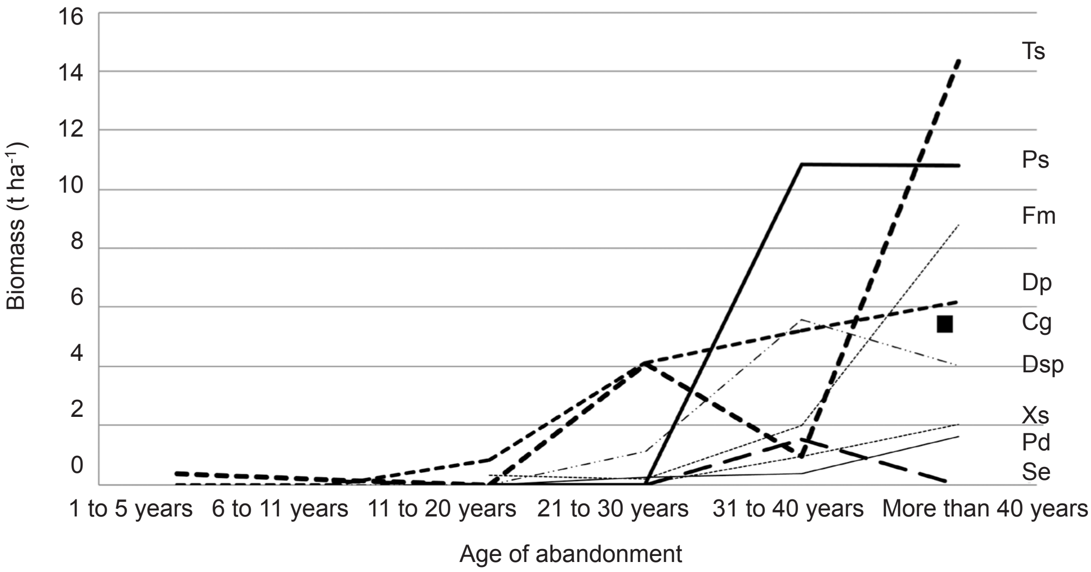

Figure 3 Mean total biomass (stems, branches, leaves) per age of abandonment (n = 5) of trees that have dry biomass (ODB) > 1 t ha^{-1} in any one of the age classes; Ts = *Tarenna sericea*, Ps = *Poupartia silvatica*, Fm = *Fernandoa madagascariensis*, Dp = *Diospyros perrieri*, Cg = *Croton greveanum* (only in the age class > 40 years), Dsp = *Dalbergia* sp., Xs = *Xeromphis* sp., Pd = *Phylloctenium decaryanum*, Se = *Stereospermum euphorioides*

Herbaceous biomass in regenerating stands

After culture abandonment, herbaceous plants in the field layer grew rapidly as shown by the quantities of dry biomass in the first five years (herbaceous air-dried biomass of 2.0 t ha^{-1}), and decreased after 20 years. This trend was due to the development of ligneous species, which allowed less light to reach the soil, and increased coverage by litter.

Soumit and Malaya (2006) studied dry deciduous forests in India and the impact of different periods of protection of degraded forest stands on species composition, phytosociological type and biomass of herbaceous vegetation. After the beginning of stand regeneration, they found herbaceous biomass values of 83.2 (after two years), 62.2 (after four years), 58.0 (after six years) and 64.0 g m^{-2} (after 10 years) (respectively 0.83, 0.62, 0.58 and 0.64 t ha^{-1}), which were less than those in our study site (2.0 t ha^{-1} in the first 5 years, and 2.4 t ha^{-1} between 6 and 10 years). In their study site, the annual rainfall was much higher (1407 mm) than that in our study (707 mm). Soumit and Malaya (2006) dried the herbaceous vegetation at a temperature of 90 °C. Our herbaceous vegetation was air dried at ambient field temperature but the samples did not significantly lose more water when oven dried at 60 °C. Therefore, this cannot explain why our values of herbaceous biomass are higher. Another explanation could be the anthropogenic activities such as clear felling of trees for timber and fuel wood, overgrazing and surface burning, which were the causes for the destruction of climax tropical dry deciduous forests in India and thus might have degraded soils more severely.

Comparison of productivity with other studied forests

In the dry forest of Yucatan, Mexico, a dry biomass of 21 t ha^{-1} was obtained after two to five years in forest recovering following shifting cultivation of maize (Read & Lawrence 2003). In the same age (1–5 years after culture abandonment), we had 0.4 t ha^{-1}. The high precipitation (900–1400 mm) and the type of soils (shallow, calcareous and highly permeable due to organic matter content and underlying limestone bedrock) were presumably the main causes of this biomass difference.

Raherison and Grougzis (2005) studied dense primary deciduous dry forests of *Dalbergia, Commiphora* and *Hildegardia* in south-west Madagascar (about 400 km south of our study site). Despite similar climate and soil types, their aboveground dry biomass was roughly twice higher (113 t ha^{-1}) than in our case (66.9 t ha^{-1} after more than 40 years after culture abandonment). This shows the contrast between virgin dry forest and secondary forests of 40 years. The aboveground biomass of dry undisturbed dense tropical forest in Mexico was studied by Martinez-Yrizar et al. (1992). They found for these forests 77.7 t ha^{-1} of dry biomass. This value is comparable to our tree biomass (ODB 66.9 t ha^{-1}) measured after 40 years. This result is surprising, given the fact that the forest studied by Martinez-Yrizar et al. (1992) had an average height of 6.9 m, which was more than in our forest (3.3–5.6 m). Our relatively high biomass value was possibly due to the drying process (60 °C in our case and 105 °C for Martinez-Yrizar et al. 1992) and to the slightly higher precipitation (791 mm against 707 mm in Mexico). On the other hand, because of shifting cultivation, the multi-stemmed trees were very dense in our older sites and this contributed much to the biomass.

With respect to rainforests in the east of Madagascar, the traditional slash-and-burn agricultural system is the dominant landuse (Styger et al. 2009). Forests or fallows are cut, burnt and upland rice is usually cultivated for one year. The land soon becomes unsuitable for cropping, and is finally abandoned. Styger et al. (2009) observed, after a fallow period of three years, a biomass of 11 t ha^{-1} for the shrub species *Psiadia alitissima* and of 8.5 t ha^{-1} for *Trema orientalis*. This is considerably larger than our value of total aboveground biomass of trees and lianas after five years of abandonment (0.4 t ha^{-1}). Again, the difference might be due to the contrasted climate between the east and west coasts of Madagascar (2000 and 3500 mm $year^{-1}$, only 791 mm $year^{-1}$ of rainfall in our study site). Saldarriaga et al. (1988) studied the aboveground biomass of rainforest in the upper Rio Negro of Columbia and Venezuela slash-and-burn cultivation. In their study, surfaces were clear-felled, burnt and used for crops for two to four years and abandoned, allowing regrowth of forest. Their soils, like ours, were poor in nutrients (oxisols and ultisols). Saldarriaga et al.(1998) found 44 t ha^{-1} in the first 10 years following slash-and-burn agriculture. Their aboveground biomass was much higher than in our case (1.2 t ha^{-1} in 6–10 years after culture abandonment and 2.5 t ha^{-1} after 11 to 20 years). The equatorial climate with yearly rainfall of 3500 mm was the reason of this contrast of biomass yield.

The above-mentioned studies used allometric equations based on dendrometric variables. In our case we used a direct method (cutting and weighing), which was probably more suited for secondary vegetation with various growth types and lower-statured trees. The exhaustive measure of biomass by means of a total harvest in one selected plot of each age class gives a validation of the calculated values with biometic measures. The calculated biomass values seemed generally lower than the measured ones (between 68 and 87%, except for age class of 31 to 40 years, where they were higher with 110%). This discrepancy can partly be explained by the selective harvests by local farmers in the period between biometric and biomass measurements and the total harvest of biomass.

Common species and biomass contribution

For the plots abandoned after 30 years, we were able to identify those species used by the local population. *Dalbergia* sp. and *D. perrieri*, which produce heavy and hard wood, are widely used for cabinet making and construction, and this explains the biomass decrease after 30 years for one of them. By contrast, *F. madagascariensis* is a species that the local population uses only for cattle fences and this does not affect the biomass over time. *Poupartia*, which settles lately, becomes a key player as it is, comparatively, the species with the highest biomass shortly after 30 years of abandonment.

CONCLUSIONS

Considering the biomass reconstitution after slash-and-burn cultivation, it becomes clear that the overall ligneous biomass continuously increases up to 40 years. Furthermore, comparisons with virgin forest in similar climates in the same region indicate the potential for the biomass to double. Early in the succession, stems represent more than 50% of the total aboveground biomass, and this increases up to 72% after 40 years. This contribution is largely due to ligneous species such as *F. madagascariensis, D. perrieri, Dalbergia* sp., *P. sylvatica, T. sericea* and *C. greveanum.* Since *Dalbergia* and *Diospyros* are targeted by local farmers, it is important to have other species able to contribute significantly to biomass. *Pourpartia* has a good potential as a major biomass contributors after 30 years. Nutrient content of the biomass of these different species is then critical for quantifying the overall inputs and benefits for slash-and-burn cultivation and this knowledge is required for optimising this traditional practice.

ACKNOWLEDGEMENTS

This study was supported by the Commission for Research Partnerships with Developing Countries (KFPE), Claraz and Antoine Foundation, International Foundation for Science (IFS), Ecole Polytechnique Fédérale de Lausanne (EPFL), Federal Institute of Technology Zurich (ETHZ) and Subvention égalité of University of Neuchâtel. We thank all the farmers in Andranolava who allowed us to work in their fields, M Sinaotsy and G Ramahatombo for organising the contacts with the farmers and helping with field summer work and T Andriambahiny for the translation.

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Appendix 1 Tree and liana frequencies in the 30 plots (numbers of individuals among a total of 1101 recorded plants) according to growth type and age of abandonment

Species	Growth type					Age of abandonment																																			
						1–5 years						6–10 years						11–20 years						21–30 years						30–40 years						> 40 years					
	I	II	III	IV	Freq	I	II	III	IV	Tot	Tot/ ha	I	II	III	IV	Tot	Tot /ha	I	II	III	IV	Tot	Tot /ha	I	II	III	IV	Tot	Tot /ha	I	II	III	IV	Tot	Tot / ha	I	II	III	IV	Tot	Tot / ha
Fernandoa madagascariensis	103	4	76	7	190	-	-	-	-	0	0	-	-	-	-	0	0	7	-	3	5	15	469	5	3	3	1	12	375	42	1	33	1	77	602	49	-	37	-	86	672
Diospyros perrieri	10	5	98	2	115	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	2	3	94	2	-	14	-	16	500	8	2	62	-	72	563	-	3	21	-	24	188
Acalypha diminuata	-	-	-	101	101	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	7	7	219	-	-	-	5	5	156	-	-	-	58	58	453	-	-	-	31	31	242
Dalbergia sp.	46	9	22	2	79	-	-	-	-	0	0	-	-	-	1	1	125	-	-	-	1	1	31	27	1	1	-	29	906	18	8	13	-	39	305	1	-	8	-	9	70
Tarenna sericea	3	1	44	11	59	-	-	-	1	1	125	-	-	-	1	1	125	-	-	-	-	0	0	3	1	6	-	10	313	-	-	7	-	7	55	-	-	31	9	40	313
Ziziphus mauritiana	25	-	11	4	40	-	-	-	1	1	125	1	-	2	1	4	500	22	-	7	2	31	969	2	-	2	-	4	125	-	-	-	-	0	0	-	-	-	-	0	0
Poupartia silvatica	10	17	9	1	37	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	1	1	31	1	-	-	-	1	31	5	9	5	-	19	148	4	8	4	-	16	125
Croton greveanum	13	4	6	11	34	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	13	4	6	11	34	266
Mussaenda arcuata	-	-	-	34	34	-	-	-	-	0	0	-	-	-	1	1	125	-	-	-	10	10	313	-	-	-	16	16	500	-	-	-	5	5	39	-	-	-	2	2	16
Xeromphis sp.	5	1	27	-	33	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	-	-	1	31	1	-	13	-	14	109	3	1	14	-	18	141
Apaloxylon tuberosum	15	1	9	4	29	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	10	1	3	2	16	500	5	-	4	2	11	86	-	-	2	-	2	16
Strychnos decussata	-	-	22	6	28	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	1	2	63	-	-	13	4	17	133	-	-	8	1	9	70
Grewia sp.	7	1	17	1	26	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	1	-	2	63	-	1	7	1	9	70	6	-	9	-	15	117
Phylloctenium decaryanum	12	-	12	1	25	-	-	-	-	0	0	-	-	-	-	0	0	5	-	-	-	5	156	2	-	1	-	3	94	1	-	5	1	7	55	4	-	6	-	10	78
Ripikala	1	-	9	10	20	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	1	2	4	125	-	-	8	6	14	109	-	-	-	2	2	16
Stereospermum euphorioides	6	1	10	3	20	-	-	-	-	0	0	-	-	-	1	1	125	-	-	-	-	0	0	2	-	1	-	3	94	3	1	9	2	15	117	1	-	-	-	1	8
Byttneria voulily	-	-	-	18	18	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	3	3	94	-	-	-	4	4	125	-	-	-	-	0	0	-	-	-	11	11	86
Clerodendron sp.	2	-	15	-	17	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	-	0	-	-	2	-	2	16	2	-	13	0	15	117
Brachylaena microphylla	14	-	-	-	14	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	14	-	-	-	14	438	-	-	-	-	0	0	-	-	-	-	0	0
Calopyxis sphaeroides	1	-	9	1	11	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	1	-	2	63	-	-	8	1	9	70	-	-	-	-	0	0

(continued)

Appendix 1 (continued)

Species	Growth type					Age of abandonment: 1- 5 years						6–10 years						11–20 years						21–30 years						30–40 years						> 40 years					
	I	II	III	IV	Freq	I	II	III	IV	Tot	Tot/ ha	I	II	III	IV	Tot	Tot /ha	I	II	III	IV	Tot	Tot /ha	I	II	III	IV	Tot	Tot /ha	I	II	III	IV	Tot	Tot / ha	I	II	III	IV	Tot	Tot / ha
Chadsia grevei	4	3	4	-	11	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	1	-	-	2	63	-	-	-	-	0	0	3	2	4	-	9	70
Cordyla mada-gascariensis	2	4	5	-	11	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	-	1	8	2	4	4	-	10	78
Isolona mada-gascariensis	-	-	11	-	11	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	11	-	11	86	-	-	-	-	0	0
Cabucala mada-gascariensis	-	-	-	11	11	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	2	2	63	-	-	-	1	1	31	-	-	-	2	2	16	-	-	-	6	6	47
Psorospermum androsaemi-folium	2	1	3	3	9	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	1	2	-	3	94	-	-	-	-	0	0	2	-	1	3	6	47
Albizia bernieri	1	-	7	1	9	-	-	-	-	0	0	-	-	-	1	1	125	-	-	-	-	0	0	-	-	-	-	0	0	1	-	5	-	6	47	-	-	2	-	2	16
Capurodendron perrieri	-	-	8	-	8	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	5	-	5	39	-	-	3	-	3	23
Jatropha curcas	7	-	1	-	8	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	2	-	1	-	3	94	3	-	-	-	3	23	2	-	-	-	2	16
Cordia myxa	4	1	2	-	7	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	4	1	2	-	7	219	-	-	-	-	0	0	-	-	-	-	0	0
Poupartia minor	2	2	2	-	6	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	2	-	2	-	4	31	-	2	-	-	2	16
Asparagus vaginellatus	-	-	-	5	5	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	3	3	94	-	-	-	1	1	8	-	-	-	1	1	8
Chloroxylon falcatum	2	-	3	-	5	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	2	-	2	-	4	31	-	-	1	-	1	8
Croton sp.	-	-	4	1	5	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	2	-	2	16	-	-	2	1	3	23
Securinega seyrigii	-	-	5	-	5	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	4	-	4	31	-	-	1	-	1	8
Terminalia boivinii	-	-	5	-	5	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	4	-	4	31	-	-	1	-	1	8
Hydrostachys maxima	-	-	3	2	5	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	2	3	23	-	-	2	-	2	16
Dalechampia clematidifolia	-	-	-	5	5	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	1	1	31	-	-	-	-	0	0	-	-	-	4	4	31
Bridelia pervilleana	2	-	2	-	4	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	2	-	3	23	1	-	-	-	1	8
Lantana camara	3	-	1	-	4	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	-	1	31	-	-	-	-	0	0	3	-	-	-	3	23
Poivrea coccinea	-	-	-	4	4	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	2	2	63	-	-	-	-	0	0	-	-	-	2	2	16	-	-	-	-	0	0

(continued)

Appendix 1 (continued)

Species	Growth type					Age of abandonment																																			
						1–5 years						6–10 years						11–20 years						21–30 years						30–40 years						> 40 years					
	I	II	III	IV	Freq	I	II	III	IV	Tot	Tot/ha	I	II	III	IV	Tot	Tot /ha	I	II	III	IV	Tot	Tot /ha	I	II	III	IV	Tot	Tot /ha	I	II	III	IV	Tot	Tot / ha	I	II	III	IV	Tot	Tot / ha
Cryptostegia grandiflora	-	-	-	3	3	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	1	1	31	-	-	-	-	0	0	-	-	-	2	2	16	-	-	-	-	0	0
Canthium sp.	-	-	3	-	3	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	3	-	3	23	-	-	-	-	0	0
Rothmannia tropophylla	-	-	-	3	3	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	1	1	31	-	-	-	-	0	0	-	-	-	2	2	16	-	-	-	-	0	0
Bivinia jalbertii	-	-	2	-	2	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	2	-	2	16	-	-	-	-	0	0
Fatsilo	1	-	-	1	2	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	1	1	8	1	-	-	-	1	8
Diospyros tropophylla	1	-	-	1	2	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	-	1	2	16	-	-	-	-	0	0
Hibiscus macrogonus	1	1	-	-	2	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	1	-	-	2	16	-	-	-	-	0	0
Mascarenhasia lisianthiflora	1	1	-	-	2	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	1	-	-	2	16	-	-	-	-	0	0
Protorhus humbertii	-	-	-	2	2	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	2	2	16
Taolakena	-	-	1	1	2	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	1	2	16
Deidamia sp.	1	-	-	-	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	-	-	1	31	-	-	-	-	0	0	-	-	-	-	0	0
Dioscorea acuminata	1	-	-	-	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	-	-	1	31	-	-	-	-	0	0	-	-	-	-	0	0
Dioscorea trichopoda	-	-	-	1	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	1	1	31	-	-	-	-	0	0	-	-	-	-	0	0
Gardenia squamifera	-	-	-	1	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	1	1	8	-	-	-	-	0	0
Pandaca sp.	1	-	-	-	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	-	-	1	8
Capurodendron sakalavum	-	-	1	-	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	-	1	8	-	-	-	-	0	0
Macrorhamnus sp.	-	-	1	-	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	-	1	8	-	-	-	-	0	0
Astrocassine pleurostylioides	-	-	1	-	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	-	1	8
Grewia voloina	-	-	1	-	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	-	-	1	-	1	8
Tamarindus indica	1	-	-	-	1	-	-	-	-	0	0	-	-	-	-	0	0	-	-	-	-	0	0	1	-	-	-	1	31	-	-	-	-	0	0	-	-	-	-	0	0
Total	310	57	472	262	1101	0	0	0	2	2	250	1	0	2	6	9	1125	34	0	11	37	82	2563	82	9	41	37	169	5281	95	24	235	95	449	3508	98	24	183	85	390	3047

Tot = total; for some species only Malagasy local names could be provided

Appendix 2 Herbaceous composition in the 30 plots according to class of age of abandonment (for some species only Malagasy local names could be provided)

Species	Family	1–5 years	6 –10 years	11–20 years	21–30 years	31–40 years	> 40 years
Commiphora lamii	Burseraceae	+	+	+	+	+	+
Kidranta		+	+	+	+	+	+
Mamaky hoho		+	+	+	+	+	+
Commelina ramulosa	Commelinaceae	+	+	+	+	+	-
Breweria sp.	Convolvulaceae	+	-	+	+	+	+
Ocimum canum	Lamiaceae	+	+	+	+	+	-
Mundulea ambatoana	Fabaceae	+	-	+	+	+	+
Sida grevioides	Malvaceae	+	-	+	+	+	+
Cyrtococcum bosseri	Poaceae	+	+	-	+	+	+
Sida rhombifolia	Malvaceae	+	-	+	+	-	+
Heteropogon contortus	Poaceae	+	-	-	+	+	+
Dioscorea acuminata	Dioscoreaceae	-	-	-	+	+	+
Indigofera tritoides	Fabaceae	+	+	+	-	-	-
Tsingirifirin'ala		-	-	-	+	+	+
Euphorbia hirta	Euphorbiaceae	-	+	+	-	-	-
Asparagus vaginellatus	Liliaceae	-	-	+	-	+	-
Turraea sp.	Meliaceae	-	-	+	-	-	+
Tacca pinnatifada	Taccaceae	-	+	-	-	+	-
Triumfetta sp.	Tiliaceae	+	-	+	-	-	-
Cissus bussei	Vitaceae	+	-	-	-	-	+
Ahi-be		-	-	-	+	+	-
Tavolo		-	-	-	+	+	-
Ramanjaitra		+	-	-	-	-	-
Rohy		+	-	-	-	-	-
Achyranthes aspera	Amaranthaceae	-	+	-	-	-	-
Tridax procumbens	Asteraceae	-	+	-	-	-	-
Cyperus rotundus	Cyperaceae	-	+	-	-	-	-
Urena sp.	Malvaceae	-	+	-	-	-	-
Macrorhamnus sp.	Rhamnaceae	-	+	-	-	-	-
Akata		-	+	-	-	-	-
Cynodon dactylon	Poaceae	-	-	+	-	-	-
Mussaenda arcuata	Rubiaceae	-	-	+	-	-	-
Ahi-daly		-	-	+	-	-	-
Vero		-	-	+	-	-	-
Solanum sp.	Solanaceae	-	-	-	+	-	-
Akatam-bivy		-	-	-	+	-	-
Telo ravy		-	-	-	+	-	-
Tsilavon-dria		-	-	-	-	+	-
Dioscorea trichopoda	Dioscoreaceae	-	-	-	-	-	+
Bozak'ala		-	-	-	-	-	+
Total		16	15	18	18	17	15