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SECONDARY SUCCESSION AND ROOT BIOMASS CHANGES IN MADAGASCAR DRY DECIDUOUS FOREST (MIKEA FOREST)

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RÉSUMÉ.— *Succession secondaire et changements de la biomasse racinaire en forêt décidue sèche à Madagascar (forêt Mikéa)*.— La structure et la distribution de la biomasse racinaire ont été caractérisées le long d'une chronoséquence de forêt secondaire (jachères âgées de 2, 6, 12 et 30 ans) et deux écosystèmes de référence (une forêt mature et une savane boisée) afin de décrire le processus de régénération de la forêt dense sèche dans le sud-ouest de Madagascar. La distribution de la biomasse racinaire en fonction de la profondeur s'ajuste bien à une fonction puissance de type $B = aD^b$ (B : biomasse racinaire en $mg.dm^{-3}$ et D : profondeur en cm). Les racines sont plus profondes dans les forêts matures et les jachères jeunes mais elles sont plus superficielles dans les vieilles jachères et la savane boisée où les sols sont plus compacts. La biomasse racinaire augmente avec l'âge de la jachère jusqu'à la douzième année et une diminution a été enregistrée dans la jachère de 30 ans. La biomasse racinaire était de 3,58 $t.ha^{-1}$ dans la jachère de 2 ans, 4,96 $t.ha^{-1}$ dans la jachère de 6 ans et 10,00 $t.ha^{-1}$ dans la jachère de 12 ans. Les valeurs de la biomasse racinaire des jachères et de la savane boisée (7,00 $t.ha^{-1}$) sont largement inférieures à celles de la forêt mature (18,5 $t.ha^{-1}$). Ainsi, le coût écologique de la déforestation dans la zone d'étude correspond une perte de 16,9 $t.ha^{-1}$ de biomasse racinaire après 30 ans d'abandon.

SUMMARY.— Root structure (distribution, biomass) was characterized along a successional chronosequence of secondary forests (2, 6, 12, and 30 years) and reference ecosystems (mature forest, woody savanna) in order to describe the recovery process of former agricultural land in south-western Madagascar. The distribution of root biomass as a function of depth fits well with a power law: $B = aD^b$ (B being the root biomass expressed in $mg.dm^{-3}$ and D depth in cm). Root distribution was deeper in mature forest and young fallows and more superficial in the old fallows and woody savanna because of higher soil compaction. Root biomass increases with the age of the fallow until the 12th year and a decrease was registered in the 30-year-old fallow. Root biomass was 3.58 $t.ha^{-1}$ in the 2-year-old fallow, 4.96 $t.ha^{-1}$ in the 6-year-old fallow and 10.00 $t.ha^{-1}$ in the 12-year-old fallow. Root biomass values in all fallows and woody savanna (7 $t.ha^{-1}$) were lower than in the mature forest (18.5 $t.ha^{-1}$). Thus, the environmental cost of deforestation in the study area corresponds to a loss of 16.9 $t.ha^{-1}$ of root biomass after 30 years of abandonment.

Tropical dry forest (TDF) can be characterized by a pattern of seasonal rainfall with dry periods of variable frequency, timing and extent. They are the most threatened terrestrial ecosystems in the tropics (Vieira & Scariot, 2006). Seventy percent of remaining TDF are considered to be at high risk and among the numerous threats, human activities and climate change (Miles *et al*., 2006). In southwestern Madagascar, due to land use conversion to slash and burn agriculture called locally *hatsaky*, 55 % of the dry deciduous forest of Mikea was cleared between 1971 and 2001 (Lasry *et al*., 2004).

The Mikea, forest people, hunter-gatherers, a little-known group of between 1000 and 3000 people live in the deciduous forest of southwestern Madagascar called Mikea forest (Stiles, 1998). In contrast to the high degree of resilience of the eastern rain forest of Madagascar (Randriamalala *et al*., 2007), post-cropping dynamics in southwestern Madagascar are characterized by transformation into savanna (Leprun *et al*., 2009; Raharimalala *et al*., 2010). After 30 years of fallow, the vegetation becomes a mixed assemblage of herbaceous and woody species characteristic of savanna (Leprun *et al*., 2009). Change in root biomass during tropical secondary succession (Glesson & Tilman, 1990; Hertel *et al*., 2003; Brearley, 2011; Lima *et al*., 2012) and its distribution in the soil profile (Jackson *et al*., 1999; Hertel *et al*., 2003) have been reviewed. Atkinson (2000) reported root properties are important factor to quantify for management of both agricultural and natural ecosystems. Many studies on above-ground biomass have been carried out in Madagascar (Styger *et al*., 2009; Raharimalala *et al*., 2012; Vielledent *et al*., 2012; Ramananantoandro *et al*., 2015); but few studies address the change in root biomass during the post-crop succession (Pfund, 2000). In particular, little is known about vertical root distribution and root biomass in the Malagasy dry deciduous forests. According to Schenk (2005), growth and distribution of plant roots are linked both to the availability of resources and to physical and biotic soil conditions. Roots play an important role in the vegetation dynamics of the extreme environments (Bai *et al*., 2010) and are essential in structural support and water and nutrient uptake (Brearley, 2011). Information on vegetation succession following slash and burn cultivation is needed to undertake the challenging work of improving land use and management of fallows. A better understanding of root biomass change is a prerequisite for the ecological restoration. Thus, the aim of this study was to describe the root recovery process of former agricultural land abandoned. We used abandoned plots of 2, 6, 12 and 30 years (noted A2, A6, A12 and A30), and compared them to woody savanna (WS) and mature forest (MF). We hypothesized that there is a relationship between root biomass and the age of fallows.

MATERIALS AND METHODS

STUDY AREA

The study area is located about 700 km south of Antananarivo at the eastern limit of the Mikea Forest, in the vicinity of the village of Analabo (22°31'50''S, 43°33'50''E, 174 m a.s.l). Mean annual precipitation is 600 mm, and mean annual temperature is 24°C. There are two seasons: the dry season from April to October characterized by monthly precipitation of less than 10 mm and the hot rainy season, from November to March, characterized by precipitation of more than 100 mm per month. The different vegetation types are mature dry deciduous forest, savanna and forest regrowth (fallows) which have re-grown after slash and burn agriculture. The soil type is Oxic Quartzipsamment (red sandy) using USDA soil taxonomy (Soil Survey Staff, 2014), it is slightly leached or unleached ferruginous tropical soil in the French soil classification (C.P.C.S., 1967), and contains 10-15% clay (Leprun *et al*., 2009). The soil chemistry and physical characteristics of the six plots were previously studied by Grouzis *et al*. (2003); they reported that the soil surface compaction increased rapidly with the age of the fallow. Soil compaction values correspond to the penetration of the penetrometer probe (0.5 cm in length) corresponding to a constant force of 70 $kgf.cm^{-2}$: 76.7 $mm/70kgf.cm^{-2}$ in A2, 37.5 $mm/70kgf.cm^{-2}$ in A6 then it stabilized in old fallows: 7.3 $mm/70kgf.cm^{-2}$ in A30 and 9.9 $mm/70kgf.cm^{-2}$ in WS. Lower penetration value indicates compacted soils. Permeability was high in the MF (1.46 $mm.s^{-1}$) and decreased progressively with the age of the fallow: values obtained for old fallow A12 (0.17 $mm.s^{-1}$) to A30 (0.09 $mm.s^{-1}$) were not significantly different from those obtained for WS (0.05 $mm.s^{-1}$).

SAMPLING DESIGN

A series of six 50 x 50 m plots in fallow of 2, 6, 12 and 30 years since abandonment (A2, A6, A12, A30), as well as woody savanna (WS) and dry deciduous mature forest (MF) were selected in the Analabo area. The six plots were selected based on the homogeneity and physiognomy of flora and the land use history. They were representative of each fallow type, forest and savanna. Each plot was separated from the next by a minimum of 200 m and a maximum of 500 m. The plot size (50 x 50 m) was larger than the minimum area required of 100 to 200 m^2 for vegetation assessment in forest regrowth and savanna in southwestern Madagascar (Morat, 1977). The MF was never cleared for agriculture and therefore chosen as the start point of the succession (Aronson *et al*., 1993) and since it was only little disturbed by human activities, it could serve as reference system. Its main use for local population is for gathering, subsistence hunting and small-scale timber harvesting. The ages of the fallow plots were established with the help of the land owners, and this information was cross-checked with several other enquiries. Inquiries using a pre-established questionnaire were made to determine the first time the forest was cleared, the cropping duration, the tillage regime, the date of abandonment of the plot, the age of fallow and the number of fires that have passed in the plot. Most fallows had the same history of cultivation: 3 to 5 cycles of maize cultivation after clear felling of the original forest. Slash and burn practice consists in slashing all trees and then letting them dry for 20 to 45 days before burning. WS, used as the end point of vegetation succession, has been mature savanna since immemorial time because of the presence of typical savanna trees such as *Poupartia caffra* (Anacardiaceae), *Stereospermum variabile* (Bignoniaceae), *Entada abyssinica* (Fabaceae) and *Gymnosporia linearis* (Celastraceae) (Koechlin, 1972).

VEGETATION SAMPLING

Floristic data were collected in the entire 50 x 50 m plots in the fallows and the woody savanna. Trees whose diameter at breast height (dbh) was ≥ 2 cm and lianas with dbh ≥ 2 cm were identified, counted, and their dbh measured. The following parameters were calculated for each plot: species richness which is the total number of species in each sampled plot, the proportion of herbaceous species, the tree density (given as number of trees per ha), the tree species relative frequency (the absolute frequency of species divided by the sum of the absolute frequencies of all species).

ROOT SAMPLING

Soil coring technique (Böhm, 1979) was adopted to collect root biomass using an auger of internal diameter of 80 mm (XOK-37 000-Lindquist International). Ten samples were taken at random points within each 50 x 50 m plot to a depth 1.5 m. Soil cores were divided into nine layers by depth: 0–10 cm, 10–20 cm, 20–30 cm, 30–40cm, 40–50 cm, 50-75 cm, 75-100 cm, 100-125 cm and 125-150 cm. The minimum distance between two cores was at least 5 m. Root biomass was sampled in April at the end of the rainy season. In the laboratory, the roots were separated from the soil particles by double sieving under a water jet. Roots were hand separated with aid of sieves (mesh sizes 1 mm and 0.5 mm), then oven-dried at 85°C for 24 h and weighed. The amount of roots is expressed in $mg.dm^{-3}$, and then converted into tons of dry matter per unit area ($t.ha^{-1}$), assuming that no roots grow deeper than 1.5m.

DATA ANALYSIS

The vertical root distribution as a function of depth was fitted with a power function $B = aD^b$ (B being the root biomass expressed in $mg.dm^{-3}$ and D depth in cm) by EASYPLOT software. Asymptote or constant of proportionality "a" indicates the quantity of roots in deep layers, while the value for parameter "b" describes the decrease in root biomass. The coefficient of determination r^2 was used to indicate how well data fit the statistical model. Based on the Gale & Grigal (1987) model, a nonlinear function $C = 100(1-\beta^D)$ was fitted to the biomass root data collected, where C is the cumulative root percentage from the soil surface to depth D in cm and β is the extinction coefficient. In this model, the values of "β" parameter provide a numerical index of root depth with high β values (e.g., 0.96) indicating proportionally more roots at depth and low β values (e.g., 0.94) proportionally more near the surface (Jackson *et al*., 1999).

RESULTS

VEGETATION STRUCTURE

The proportion of herbaceous species increased up to the 12th year after abandonment: 20% in A2 to 29.2% in A12 then decreased 20% in A30 (table I). There is no herbaceous layer in MF. The tree density followed the same pattern up to the 12th year (6976 individuals ha^{-1}) and then decreased (3380 individuals ha^{-1} in A30). WS has tree density (4508 individuals ha^{-1}) similar to that found in old fallow (A30) but lower than in MF (8628 individuals ha^{-1}).

TABLE I

Principal tree species in bold type (relative frequency in brackets), species richness (S), percentage cover of herbaceous species and tree density (D)in the sampling sites

Sites	Main species	S	Herb. (%)	D ($N.ha^{-1}$)
MF	***Gyrocarpus americanus* Jacq**. (6.8), ***Diospyros manampetsae* H. Perr**.(6.4), ***Croton elaegni* Baillon** (6.4), ***Baudouinia fluggeiformis* Baillon** (6.1), ***Euphorbia laro* Drake** (4.7)	140	0	8628
A2	***Diospyros manampetsae* H. Perr.** (30), ***Hippocratea urceolus*** Tul. (18), ***Alchornea humbertii* Leandri** (12), *Dactyloctenium aegyptium* (L.) Willd. (10), *Cenchrus biflorus* Roxb. (8)	86	20	5984
A6	***Fernandoa madagascariensis* Spague** (29), ***Diospyros humbertii* H. Perr**. (26), ***Hippocratea urceolus* Tul.** (14), *Sesbania punctata* Du Puy et Labat (12), *Boerhavia diffusa* Linn (10).	67	23.9	6440
A12	***Fernandoa madagascariensis* Spague** (55), ***Alchornea humbertii* Leandri** (18), ***Diospyros humbertii* H. Perr**. (6), *Brachiaria reptans* (Trin) Griseb. (15), *Tridax procumbens* Linn. (10)	65	29.2	6976
A30	***Fernandoa madagascariensis* Spague** (33), ***Rhopalocarpus lucidus* Boj.** (13), ***Tamarindus indica* Linn.** (5), *Heteropogon contortus* (L.) P. Beauv. ex Roem.& Schult (25), *Sporobolus* sp. (5)	64	20	3380
WS	***Stereospermum variabile* H. Perr.** (30), ***Poupartia caffra* (Sond.) H. Perr.** (15), ***Entada abyssinica* Steud. Ex A. Rich** (11), *Heteropogon contortus* (18), *Cyperus* sp. (3)	73	27	4508

MF: Mature Forest; A2: fallow 2 year-old, A6: fallow 6 year-old, A12: fallow 12year-old, A30: fallow 30 year-old; WS: Woody savanna.

In the savanna, woody species associated with the grass *Heteropogon contortus* are mainly *Poupartia caffra*, *Stereospermum variabile* and *Entada abyssinica*. The proportion of herbaceous species is high (27 %) in the savanna due to the abundance of grass species.

ROOT BIOMASS

The highest root biomass was recorded in mature forest (18.5 $t.ha^{-1}$) and the lowest in 2-year-old fallow (3.58 $t.ha^{-1}$) (Fig. 1). Root biomass in mature forest is significantly different to fallows and WS.

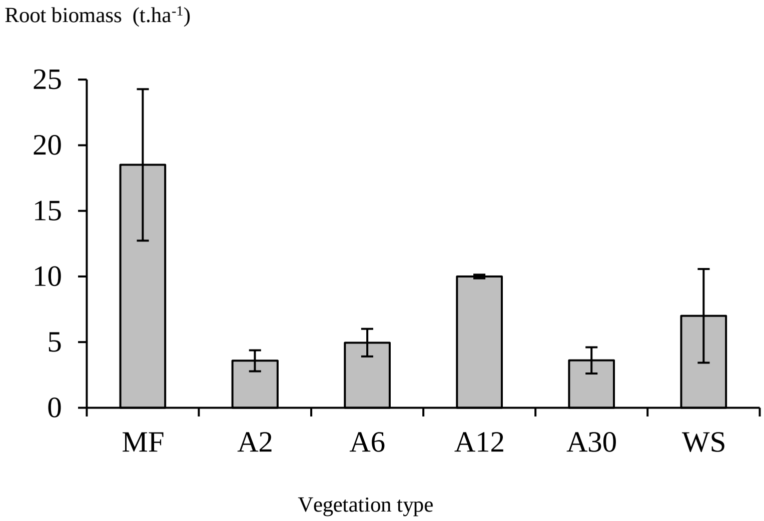

Figure 1.— Root biomass ($t.ha^{-1}$) in 1.5 m depth. MF: Mature Forest; A2: 2-year-old fallow, A6: 6-year-old fallow, A12: 12-year-old fallow, A30: 30-year-old fallow; WS: Woody savanna.

Root biomass increased with the age of the fallow: very low in A2, it increased to 4.96 $t\ ha^{-1}$ in A6, and reached a value of 10.0 $t\ ha^{-1}$ in A12. After 12 years, a rapid decrease in root biomass was observed, down to 3.6 $t\ ha^{-1}$ in 30-year-old fallow, a value comparable to those obtained in WS.

VERTICAL ROOT DISTRIBUTION

Root biomass generally decreased with depth. All R^2 coefficients of determination are high and vary from 0.85 to 0.95 (Fig. 2).

The slopes of the root vertical distribution curves for the MF and the young fallow (2-year-old fallow-A2) are lower than those for A30 and WS. Thus, MF and A2, with high "a" values (7443 and 13135 respectively), had the largest quantities of root biomass across depth. Inversely, low "a" values were obtained in 30-year-old fallow (2248) and in WS (3082) and intermediate values corresponded to fallows falling between 6 and 12 years.

The decrease in root biomass, which was relatively slow in recent fallow (A2 and A6), was characterized by high "b" absolute values (-1.080 and -0.899). In old fallows (A12 and A30) and in the savanna, "b" values were between -0.760 and -0,780, resulting from a much more rapid decrease in root biomass as a function of depth. The forest presented intermediate (-0.764) "b" value.

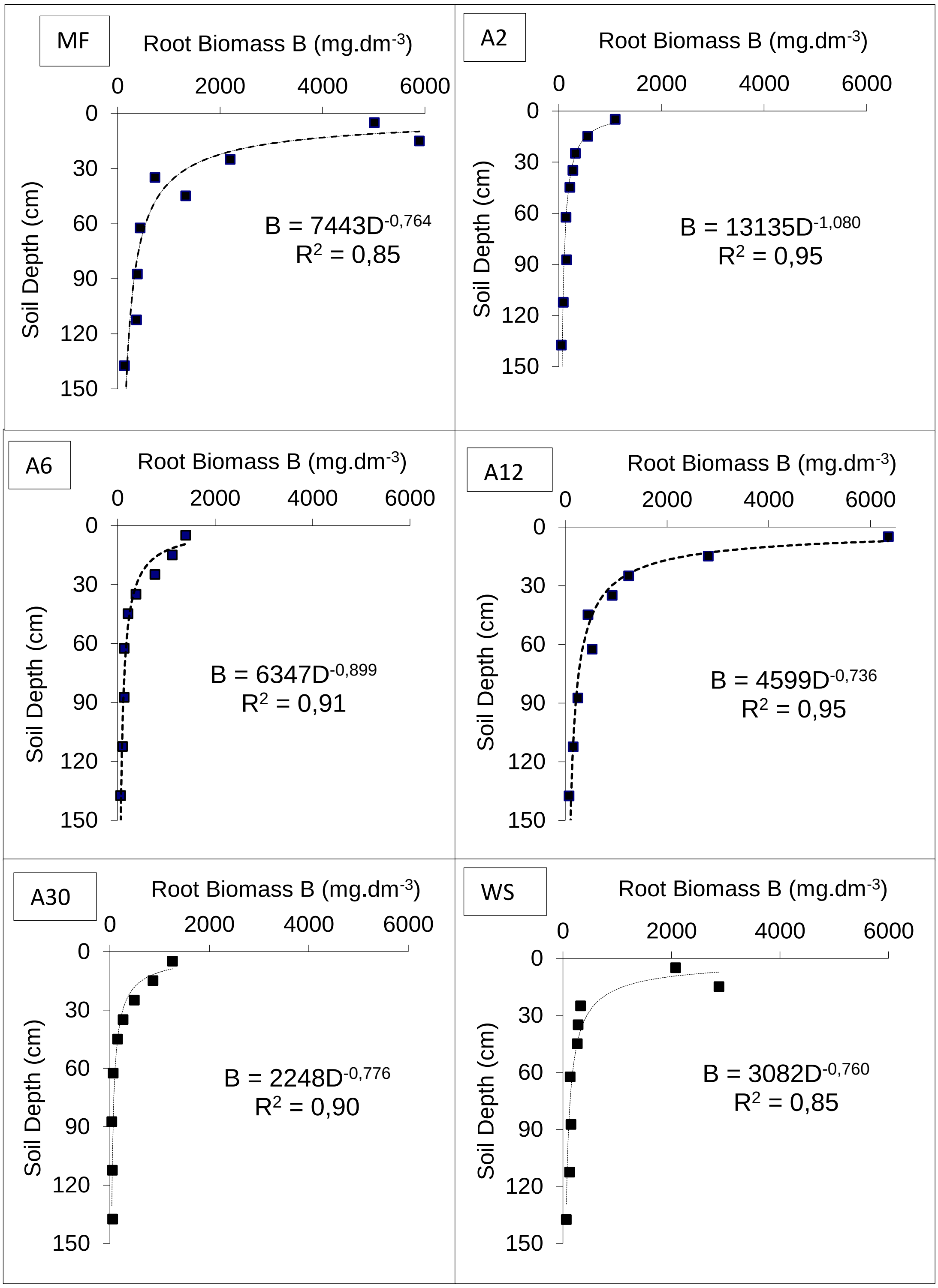

Figure 2.— Vertical root distribution curve $B = aD^b$ [B: Root Biomass ($mg.dm^{-3}$), D: Depth (cm)], MF: Mature Forest; A2: 2-year-old fallow, A6: 6-year-old fallow, A12: 12-year-old fallow, A30: 30-year-old fallow; WS: Woody savanna.

CUMULATIVE ROOT BIOMASS WITH DEPTH

Figure 3 shows variations in cumulative percentages (C in %) of the root biomass as a function of depth based on the Gale & Grigal model $C = 100(1-\beta^D)$, where D is depth (in cm), R is the cumulative root fraction from the soil surface to depth d and β is the extinction coefficient (Gale & Grigal, 1987). In this model, the values of "β" parameter provides a numerical index of root depth with high β values (e.g., 0.96) indicating proportionally more roots at depth and low b values (e.g., 0.94) proportionally more near the surface (Jackson, 1999). The root distribution of MF and the young fallow is deeper than that of 30-year-old fallow and WS. The first 30 cm of soil contained 75 %, 70 %, and 74% of roots in MF, A2 and A6 respectively; 79 % of the roots in A30; and 82 % of the roots in the WS (Fig. 3).

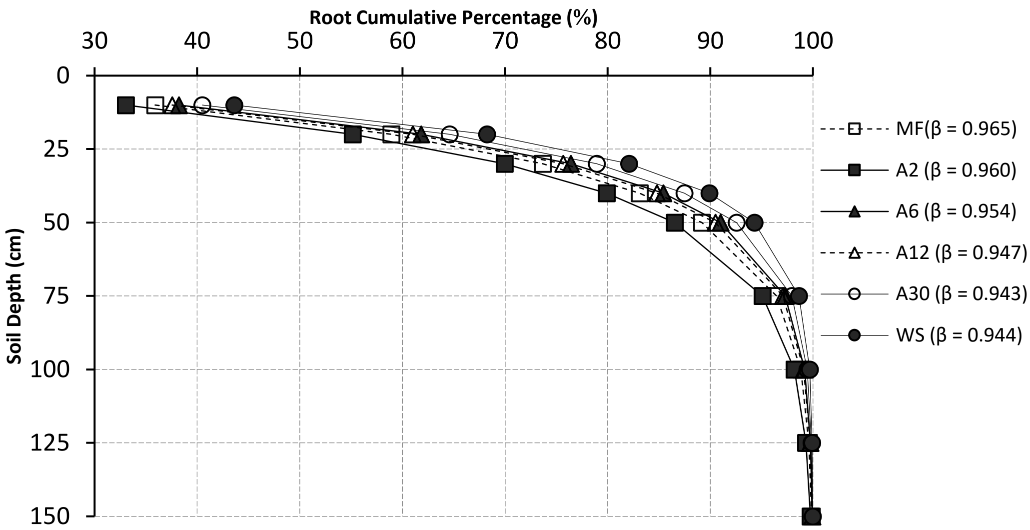

Figure 3.— Cumulative percentages (%) of the root biomass as a function of soil depth (cm). MF: Mature Forest; A2: 2-year-old fallow, A6: 6-year-old fallow, A12: 12-year-old fallow, A30: 30-year-old fallow; WS: Woody savanna.

It is possible to distinguish recent fallows (A2, A6, and A12), where less than 90 % of the roots are found in the 0-50 cm layer, from old fallow and WS where this value is greater than 90 %. The values for the forest are intermediate. Across all plots, the upper 75cm of soil contained at least 95 % of root biomass.

DISCUSSION

The main findings of this study are (i) most root biomass (85 to 95 %) was concentrated in the upper soil layer (0-50 cm) and (ii) the general trend in succession showed that root biomass, vegetation structure and soil characteristics are influenced by fallow age and land use management: root biomass increased with fallow age due to increasing tree density and decreased with recurrent fire and soil compaction.

BELOW-GROUND ROOT BIOMASS

In terms of production, the values for below-ground root biomass obtained in fallows and savanna are considerably lower than in mature forest. The lowest values were observed in A2 ($3.58\ t.ha^{-1}$) and A30 ($3.61\ t.ha^{-1}$). This is due to the low density of woody species in these sites. The high value of tree density in the MF is associated with a large value of the basal area due to the abundance of larger trees with diameter at breast height (DBH > 10 cm). Larger trees with basal area = 16.6 $m^2.ha^{-1}$, contributed over 95 % of the total basal area (19.6 $m^2.ha^{-1}$) in the MF in the same site (Raherison & Grouzis, 2005). However, basal area (9.6 $m^2.ha^{-1}$) is low in old fallow A30 that is composed of shrubs and scattered trees (Randriambanona *et al*., 2015).This difference is attributed to difference in land management, the fallows are subjected to grazing pressure and fire. Mitja (1992) in Ivory Coast and Manlay *et al*. (2000) in Senegal obtained similar results. They also underlined the fact that woody species contribute the most to below-ground root biomass. Mean root biomass in young fallow (A2 and A6) is 4.2 $t.ha^{-1}$; which is lower than values given in Manlay *et al.* (2000) for fallows in Senegal (4 to 7 $t.ha^{-1}$). Values for root biomass in the savanna of southwest Madagascar (poor in woody species) are considerably lower than those obtained in the savanna in Ivory Coast which vary from 10 to 19 $t.ha^{-1}$ in only 30 cm of top soil (Fournier, 1991). It is noted that the type of vegetation alone is not enough to enable values for below-ground root biomass to be interpreted, as soil and climatic conditions can also have a modifying effect. Our mature forest root biomass value (18.5 $t.ha^{-1}$) is similar to that found by Raherison & Grouzis (2005) in a mature forest growing on light reddish sands (17.8 $t.ha^{-1}$) in the same study site. However, these values are lower than those recorded in rainforest in Ivory Coast (23 to 25 $t.ha^{-1}$) characterized by high tree density (Huttel & Bernhard-Reversat, 1975). We also observed that root biomass increased with the age of fallows up to A12. This increase may be due to the density of woody species, which increases with the age of the fallow (Delang & Li, 2013). A number of studies have reported similar trends: e.g. Mora *et al*., (2017) in dry deciduous forest in Mexican Pacific coast. Martin *et al.* (2013), using meta-analysis data from more than 600 secondary tropical forest sites showed that root biomass took longer to recover compared to above-ground. In our study site, after the 12^{th} year, there was a distinct drop in root biomass, which is evident for old fallow (A30) and savanna. Root biomass was 3.6 $t.ha^{-1}$ in the 30-year-old fallow, although this value still lies within the normal range for savanna root biomass: 2.6 $t.ha^{-1}$ for grass savanna (Grouzis *et al*., 2003) and 7 $t.ha^{-1}$ for WS. The drop is due to the low density of woody species in A30 as well as to soil characteristics (compaction and a decrease in the permeability of the surface horizons), which prevent plants from developing their root systems. The major effect of soil compaction in the savanna and the old fallows is manifested in decreased soil permeability and increased mechanical resistance that inhibited root growth. According to Jacovac *et al*. (2015), land use intensity such as weeding, age of previous fallow, number of fallow cycles, determined the recovery of forest structure.

VERTICAL ROOT DISTRIBUTION

Distribution of root biomass as a function of depth showed that the quantity of roots decreased rapidly with depth in all the studied vegetation types and fallows according to a power law distribution. The model of distribution is identical for all the plots despite differences in the density of woody species between sites. This characteristic is similar to the finding of Menaut & César (1982) in West African savanna, these authors underlined the fact that the pattern of root biomass distribution is not influenced by the density of trees and shrubs. In young fallow (A2), high density of sprouters contributes to maintain high root biomass and the many dead roots may have not yet decomposed and are therefore included in our measures.

Root biomass was mainly concentrated in the surface layers in old fallow (A30) and WS. The values of "a" are low and are similar to those obtained by Fournier (1991) in shrub savanna in west Africa (a = 3110). In parallel to the marked concentration of roots in the surface layers, there was a rapid decrease in root biomass with depth. This characteristic can be explained by the physical properties of the soil. According to Olupot *et al.* (2010) soil organic carbon (SOC) tends to be concentrated in the topsoil where the highest fine root biomass is located. These soils have superficial dynamics due to hardening layers that tend to reduce permeability. The dense cover of perennial grasses such as *Heteropogon contortus* may also be the cause of the concentration of roots in the surface layers (Jackson *et al*., 1999).

Root distribution in the mature dry deciduous forest in southwest Madagascar is comparable with that in the deciduous tropical forest studied by Jackson *et al.* (1999) (mean β value: 0.961). In our study, root distribution was deeper in forests and young fallow (β values range from 0.954 to 0.960) and distinctly more superficial in savanna-type stands (β value: 0.944). In savanna, soils become compacted because of cattle grazing, so roots have difficulty to penetrate and therefore concentrate in the surface soil layer. It thus appears that root distribution becomes progressively shallower during post-agricultural succession. It is possible to distinguish recent fallows (A2, A6 with β values which range from 0,954 to 0.960), where root distribution is still comparable with the reference forest system (β value of 0.965), from savanna-type ecosystems (A30, WS :β values range from 0.943 to 0.944), where root formation is more superficial. In the latter, the top 50 cm of soil contain over 90 % of the roots. These results are similar to those reported by several authors who found a highest vertical root distribution of below-ground root biomass towards the upper 50 cm of the soil profile (Pucheta *et al*., 2004; Rueda *et al*., 2010). Soil water availability is the important environmental parameter in TDF (Costa *et al*., 2014). An important point to note here is that vertical root distribution could be explained by the plant functional trait classified in three basic groups: trees, shrubs, and herbaceous. Trees species deploy a greater of their root biomass deeper in the soil profile where water is available. The shallowest rooting life form is herbaceous (Jackson *et al*., 1996). Without alternative land management, the fallow's transformation into savanna will aggravate the problems of soil degradation. Useful and necessary objectives for restoration of soil fertility would be improved management by developing e.g. intercropping bean-maize-cassava that would increase food crop production and contribute to soil sustainability. If the fallows are protected against fire, regeneration is possible and they evolve towards forest stages. Randriambanona *et al*., (2015) showed in the same site that structure (tree height, canopy cover) in old fallows (23 and 27 year) and mature forest is similar while floristic composition is different. However, it was difficult to determine the time that fallows need to reach similar species composition as the mature forest.

CONCLUSION

The distribution of roots enabled a distinction between young fallows (A2, A6) characterized by a deeper root system similar to that found in mature forest, and old fallow (A30) characterized by more superficial roots, similar to that of WS. In young fallows, herbaceous plants that are the first to establish, associated with resprouting woody species, play an important role in root distribution. In old fallows and WS, the root system is mainly represented by that of perennial grasses. These biological features are accompanied by change in soil physical properties, notably by the hardening of the surface. Our results contribute to the understanding of fallow and slash and burn agriculture and have implications for planning and management restoration efforts in abandoned fields or fallows at regional levels. For example: it may be important to consider planting first early successional pioneer species allowing natural successional mechanisms to proceed, and mature species can be introduced in mid-and old successional where they are more likely to establish and survive.

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