Successional dynamics of tree species during forest recovery in the southeast of Côte d'Ivoire

Common title : **Forest successional dynamics**

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Abstract

Secondary forests constitute currently a large and growing component of forest cover, and can be found to be very important for a wide range of goods and services. A synchronic study has been achieved about successional stages in the forest recovery in the Southeast of Côte d'Ivoire. The objectives were to determinate trees species diversity at different sucessional stages and the auto-ecological characters of the most abundant species following abandonment of agricultural areas. Tree species with dbh ≥ 2.5 cm were counted in 85 plots from fallows gradient and 20 plots from two old-growth forests as control. Five successionnal stages were identified based on patch occupancy of the 10 best competitor / colonizer advantages. Tree species richness and diversity were significantly higher in the oldest forests. During the first 30 years of secondary regrowth, richness and diversity profile have not been influenced by age since abandonment. At least 14 % of forest tree sepcies were surveyed in young fallows. From two to five pioneer, non pioneer light demanding and shade-tolerant species have the most abundant accoding to successionnal stages. Sixty percent of these species were confined to the Guineo-Congolian region and at least 80 % of diaspores were sarcochory and sclerochory types. This study shown that farmers practices in the rural area, were favorable to forest recovery in terms of faster regeneration after agricultural abandonment. This rapid forest recovery can provide the availability of farmlands and can be a good opportunity for human pressures reduction on protected forests.

Key words : successional dynamics, fallows, forest disturbance, auto-ecological character, Yapo protected forest

Résumé

Dynamique de succession des especes arborescentes pendant la reconstitution forestiere au sud-est de la cote d'ivoire

Titre courant : **Dynamique de sucession forestière**

Les forêts secondaires constituent actuellement une composante importante de la couverture forestière, et peuvent être considérées comme très importantes pour une large gamme de biens et de services écosystémiques. Une étude synchronique a été réalisée sur les stades de succession dans la reconstitution forestière au Sud-est de la Côte d'Ivoire. Les objectifs étaient de déterminer la diversité des espèces d'arbres à différents stades et des caractères autoécologiques des espèces les plus abondantes, après abandon cultural. Les espèces d'arbres avec un dbh ≥ 2,5 cm ont été comptées dans 85 parcelles issues d'un gradient d'âge de jachère et 20 parcelles issues de deux forêts anciennes prises comme témoin. Cinq stades successifs ont été identifiés en fonction des abondances des 10 meilleures espèces colonisatrices / Compétitrices dans les parcelles. La richesse et la diversité des espèces étaient significativement plus élevées dans les forêts anciennes. Au cours des 30 premières années de reconstitution, le profil de diversité des espèces n'est pas influencé par l'âge des jachères. Au moins 14% des espèces rencontrées dans les forêts anciennes, sont présentes dans de jeunes jachères. Deux à cinq espèces pionnières, non pionnières ou tolérantes à l'ombre, ont les plus fortes abondances selon les stades de succession. Soixante pourcent de ces espèces sont endémiques à la région Guinéo-Congolaise et au moins 80% des diaspores étaient des types sarcochore et sclérochore. Cette étude a montré que les pratiques agricoles au Sud-est de la Côte d'Ivoire, sont favorables à un rapide rétablissement des forêts. Cette reconstitution forestière peut assurer la disponibilité des terres agricoles en zone rurale et peut être une bonne opportunité pour la réduction des pressions humaines sur les forêts protégées.

Mots clés : Dynamique successionnelle, Jachères, perturbation forestière, caractères autoecologiques, Forêt classée de Yapo, Côte d'Ivoire

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INTRODUCTION

The West African moist forests have been reported as rich ecosystems with complex structures which contain many notable endemic species (Sayer et al., 1992). However, forests in this region of the world are under serious threats. According to the Food and Agricultural Organization of the United Nations (FAO, 2016), the annual rate of deforestation in the region has been estimated at 4.2 million ha per year from 1990 to 2000 and at 2.7 million ha per year from 2000 to 2015.

In this region, with past and continued destruction of primary forests, secondary forests constitute a large and growing component of forest cover, and can be found to be very important for a wide range of goods and services. These secondary forests, such as in many others troipical regions, are subject of an increasing interest (Smith et al., 1999, de Jong et al., 2001). This is mainly, the forests that have naturally regenerated after anthropogenic disturbance (Chazdon et al., 2007). These secondary forests currently, constitute a large proportion with 90 % of West Africa's forests cover (Schroeder et al., 2017). They contribute to biodiversity conservation by relieving pressure on primary forests, by functioning as corridors for the migration of flora and fauna in fragmented landscapes, and by maintaining plant and animal genetic resources (FAO, 2006). If properly managed, they have the potential important environnemental benefits and services.

In Côte d'Ivoire, until 1935, tracts of virgin forest could still be seen when travelling along the roads (Aubreville, 2015). But, the expansion of cocoa, coffee, rice crops and also the forest clearing have involved the rarety of the primary forest in the South of the country (Aké-Assi, 1998 ; Chatelain et al., 2004). Currently, some more or less intact forests are under protection, such as the Taï National Park and the Azagny National Park. As the area of secondary forests in Côte d'Ivoire is expanding and represents the major forest type, the conservation of only old-growth forests in national parks and other protected areas, will hardly be sufficient. Indeed, the expanding secondary forest may mitigate extinction caused by declining areas of old-growth habitats (Wright and Muller-Landau, 2006). The conservation of secondary forests, which potentially contain a significant proportion of biodiversity, appears so to be timely and imperative.

Generally after disturbance, the regeneration and secondary succession of tropical moist forests is rapid in terms of species richness, plant growth, and other developmental features (Murphy and Lugo, 1986). But, successional processes are not always directional or predictable, and multiple pathways can lead to a range of mature forest types rather than a single stable endpoint (Gleason, 1926). Indeed, successional changes in richness and diversity may be driven by several stages and intrinsic species auto-ecology character differences such as recruitment, growth and mortality rates (Richards, 1952).

In Côte d'Ivoire, despite the increasing area of secondary forests (Aubréville, 2015), the forest recovery process in relation to fallows time, remains poorly explored. This study tryed to answer this question: what processes are underlying natural regeneration on abandoned agricultural lands ? The analysis focused on the determination of the sucessional stages and the auto-ecological characters of the most abundant trees species following abandonment of agricultural fields in the Southeast of Côte d'Ivoire where the agricultural has affected 71 % of forest cover (Etc Terra, 2016). The objectives of the study were : (1) to identify the successional stages based on age that both early and late successional species are able to persist during the reconstitution of forest landscape, (2) to determine the diversity and the most abundant of early and late successional species, and (3) to characterize some auto-ecological characters of these most abundant species.

METHODS

Description of the study area

The study took place around the locality of Azaguié in the Southeast of Côte d'Ivoire (Figure 1). Despite the bigest deforestation rate (71 %) in the Southeast (Etc Terra, 2016), Azaguié area supports yet, one of the largest and only block of the rainforest remains: Yapo Protected forest (YPF). Also, there are many perennial crop types cultivated according to farmers' empirical practrices in this area (Vroh et al., 2017). Among these crop farms, cocoa (Theobroma cacao), cola (Cola nitida), teck (Tectona grandis) and rubber (Hevea brasiliensis) take the larger place in the landscape. The secondary forests studied here, resulted mainy after abandonment of these crop farms.

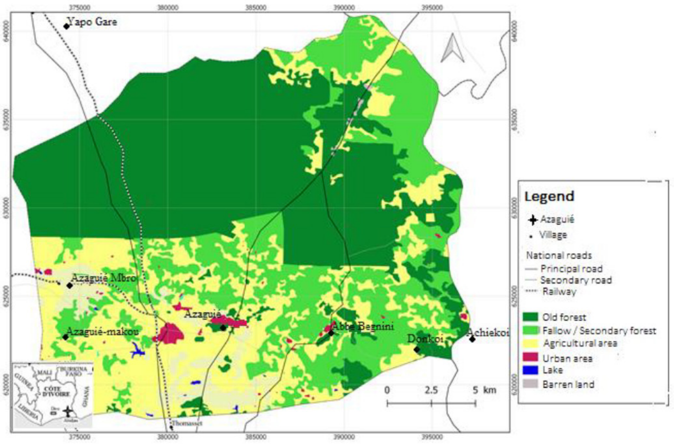

Figure 1 : Map of land use in Azaguié area
(Source: Poorter et al., 2004)

Rainfall and temperature database from 1996 to 2009 showed that, climate regime for this area had four seasons : two dry and two rainy seasons. The duration of the dry season was less than 5 months. Annual rainfall varied between 1,500 and 2,000 mm. In 1907, Chevalier was the first botanist who inventoried in this area (Corthay, 1996). The vegetation of the area is characterized by *Diospyro-Mapanietum* association (Mangenot, 1955). The main vegetation is evergreen rainforest (Guillaumet, 1967) that is being replaced by disturbed biotopes such as farms, fallows and secondary forests.

In the area the old-growth forests included the Yapo Protected Forest (YPF) and a Voluntary Natural Reserve (VNR). The two forests are differently managed. YPF was subjected to logging with enrichment in some compartments (experimental plots) which resulted in changes in its vegetation and natural flora (Corthay, 1996). The VNR is a private forest patche created by an individual. In this forest any intervention of local people was prohibited since 2005 (Vroh et al., 2010).

There were also secondary forests which included all small patches in the agricultural landscape. They are constantly penetrated by people for various reasons. These included « community forest » fragments. In these secondary forests, the farmers' activities of harvesting non-timber forest products (NTFPs) were uncontrolled and difficult to measure. According to the farmers, the fallows concerned all resting sites which have not reached optimum fertility conditions for agriculture. These fallows resulted from activities such as cocoa, cola, rubber, and teak smallholder farming systems. For this study, three biotope types (fallows, secondary forests and old-growth forests) have been selected for botanical investigation (Figure 1).

Data collection

This study based on secondary successions has be done under the synchronic approach (Tchiengué, 2012). The searching of fallows and their ages was one of the most difficult step for the approach during this study. This step was achieved through the commitment of farmers who are owners of fields. On the site, the farmer showed the fallows / secondary forests and answered questions regarding when the farm was abandoned. This reasoning allowed to select 17 habitat types including fallows and secondary forest of 1 to 45 years old. The two remainning old-growth forests (YPF and VNR) were additionnaly selected. These two sites were considered as control old-growth forests without any history of major disturbances in the area and their age was estimated more than 60 years. In the case of the present study, only Yapo Protected forest's compartments without logging activities and enrichment, were carefully selected and inventoried.

Survey was conducted using stratified sampling method. Each habitat type was considered as a stratum and plots were randomly set up. A total of 105 plots of 500 m^2 were sampled and inventoried in the YPF (N = 10 plots), the VNR (N = 10 plots), the young and old fallows (N = 85 plots). In each plot, all trees with a dbh (diameter at breast high) greater or equal to 2.5 cm, were identified, measured, and counted. Only trees with dbh ≥ 2.5 cm have been included because trees of small size contribute more to the vast majority of plant diversity (Tchouto, 2004). The dbh ≥ 2.5 cm has then been taken in the objective to take into account the maximum species and individuals. Identification of species was made on field according to Cronquist (1981) classification system. Undetermined specimens (less than 2%) were identified by Laurent Aké-Assi and by comparison to those of the National Herbarium of Côte d'Ivoire (*Herbarium ivorensis* UCJ).

Data analysis

Identification of the sucession stages

It is recognized that forest recovery followed mainly some sucessional stages based on the chronosequences and/or the most dominant species or group of species (Ruiz et al., 2005 ; Norden et al., 2015). Here the sucession stages were identified from the multispecies competition-colonization tradeoff (Pacala and Rees, 1998). According to Tilman (1994), this competition-colonization trade-off is currently the most visible explanation of successional diversity. The process is based on the multispecies "patch-occupancy models" (Caswell and Etter, 1993) in an area with several sites. Lehman and Tilman (1997) showed that this model induce more species coexistence if the competition-colonization trade-off is reached based on some references values: best competitor abundance at least 20 % ; mortality rate aqual to 10 %. Indeed, each succession stage is characterized by the dominance of one or a group of better colonizer species or better competitor's species. At plot level, the trade-off result from a constant presence of an unoccupied areas during the forest recovery process (Lett et al., 1999). These unoccupied area are therefore, favourable to species eliminated by best colonizer / competitor's species. To advoid extrapolation of the result, each curve was stoped at the maxima estimated age (60 years) of the habitats. This analysis was done with EcoVirtual Package (Stevens, 2009) for R.

Floristic description of the different sucession stages

Firstly, to illustrate how many tree species are shared between the different sucessional stages, a Venn diagram was drawn with the Bioinformatics & Evolutionary Genomic Tool (http://bioinformatics.psb.ugent.be/webtools/Venn/).

Secondly, considering the different succession stages, many diversity indices were calculated to compare trees species diversity: Species richness, Shannon, Pielou's evenness, Simpson (See Kent and Cooker, 1992 for formula details).

Thirdly, considering the fact that since a single diversity index will not provide sufficient information (Morris et al., 2014), the Renyi diversity profile was calculated. That is one of the techniques for diversity ordering and specifically designed to rank communities from low to high diversity (Kindt et al., 2006). Renyi diversity profile values (*Hα*), based on 100 randomisations, are calculated from the frequencies of each component species and a scale parameter α ranging from zero to infinity (Legendre and Legendre, 1998). The mathemathical formula of *Hα* is :

$$H\alpha = \frac{\ln \sum (pi)\alpha}{1-\alpha}$$

In this formula, *pi* is the abundance of species i and α is a scale parameter.

Legendre and Legendre (1998) and Shaw (2003) have demonstrated that values of the Renyi profile at the respective scales of 0, 1, 2 and ∞ are related to species richness S, the Shannon diversity index *H*', the Simpson diversity index and the Berger–Parker diversity index. The Berger-Parker index of dominance is the proportion of the most common (abundant) species in the community or sample and the inverse of this index is used as an index of diversity. An increase inverse of Berger-Parker index means increasing diversity and then the reduction in dominance of one species (Berger and Parker, 1970). Considerind the comparaison based on the Renyi diversity profile, community A is more diverse than a community B if the diversity profile for community A is everywhere above the diversity profile for community B (Kindt et, al. 2006). Communities that have intersecting profiles have the same diversity level. In other words, Renyi diversity ordering is a graphical method of diversity ranking that allows to distinguish between situations where ecological communities (such as successionnal stages in this survey) can be ranked in diversity or situations where this is not conceptually possible (Magurran, 1988 ; Purvis and Hector, 2000).

Finally, using the rank abundance analysis, the diagnostic species of each fallowstage were identified. For these species, we determined three auto-ecological characters (Tchiengué, 2012) : phytogeographical distribution, types of diaspore's dispersal, and regeneration guilds. The phytogeographical distribution types were inspired from White (1983). For this study, we distinguished in Africa, the Guineo-Congolian (GC) species, the Soudano-Zambezian species (SZ) and the species common to Guineo-congolian and sudano-zambezian regions (GC-SZ) between these two areas. All species outside of theses areas have been considered as exotic. Among the Guineo-Congolian species, we have distinguished those endemic to Guineo-Congolian West forest (GCW). The types of diaspore's dispersal were determined according to the classification of Dansereau and Lems (1957) which had been widely used in tropical Africa (Mosango and Lejoly, 1990; Sonké, 1998). The guild category of different most abundant species was identified considering the classification established by Hawthorne and Abu-Juan (1995). These authors recognize three categories of plants: the pioneer trees, the non pioneers light demander species and the shade-tolerant species.

RESULTS

In total 4607 trees individuals (dbh ≥ 2.5 cm) belonging to 196 species, 97 genera, and 52 families were censused in the 19 sites aged from 1 to 60 years. The number of species ranged from 2 in fallows of one year old to 166 in older forests. The most rich families were Rubiaceae (17 species), Apocynaceae (12 species), Euphorbiaceae (9 species) and Fabaceae (6 species). In all habitats, at least 50 % of species were endemic to Guineo-Congolian area. From 23.5 to 37 % of species were endemic to Guineo-Congolian and Soudano-Zambezian transitional phytogeographical area.

Succession stages and the florsitic diversity

Five (5) successional dynamics sequences have been ranked based on the patch occupancy (occurrence ≥ 10 % of plots) of the 10 best competitor / colonizer advantages (Figure 2). The first sequence concerned habitats aged from 1 to 10 years. This sequence is dominated by 5 best colonizer species. The second sequence concerned habitat that aged from 10 to 20 years. This sequence is dominated by only one species (occurrence ≥ 10 % of plots) which mark the transition between best colonizer and best competitor species. The last three sequences were dominated by best competitor species. These sequences concerned all habitats characterised by the chronosequences [20 – 30 years [; [30 – 50 years [and [50 – 60 years]. These sequences were also charcaterised by species which competitive dominant value was increasingly greater with the forest age.

Based on these five chronosequences, the species richness ranked from 166 in old forest (60 years) to 19 in old follows with 20 – 30 years (Table I).

The Nonsymmetric Venn diagram (Figure 3) showed that, 14 species (7.14 %) are shared between all the five chronosequences. Among the 36 recorded species in the young follows [1 – 10 years [, seven (19.4 %) were strictly present in these habitats. These species were not recorded in the other habitats. For the sequence [10 – 20 years [, only two species were strict. All species censused in the old follows [20 - 30 years [were also recorded in at least one other sequence. The old forests (60 years) and the oldest fallows (30 – 50 years) shared more species (64). Old forests showed 95 unique species and the oldest fallows showed 16.

The total value of Shannon index is 3.97 and ranking from 3.94 in old forest to 2.38 in secondary forest. The correspondance Eveness index in all habitat types was 0.75. The lower values of Eveness (0.73 and 0.77) were reached in the old forest and the oldest fallows. The higher value (0.82) was reached in the younger fallows with 1 – 10 old. The Simpson diversty index slightly differed between the five chronosequences (Table I).

The diversity profiles of each successional dynamic sequences are represented by Figure 4. The profile of the old forests is consistently higher than other sequences for all values of alpha. The values of species richness at H ($\alpha = 0$) are cleary different except those between the first two younger fallows (1 - 10 and 10 – 20 years) which are still rather tight. The curves became more tight for Simpson diversity Index at H ($\alpha = 2$) between the younger fallows (1 – 10 years) and oldest fallows (30 – 50 years). For Berger–Parker diversity index at H ($\alpha = \infty$), excepted old forests, the curve from all other chronosequences stay tight.

Finally results from the comparison based on the diversity profiles, showed that all successional stages have a clear bend towards low values of H-alpha at higher scales of alpha.

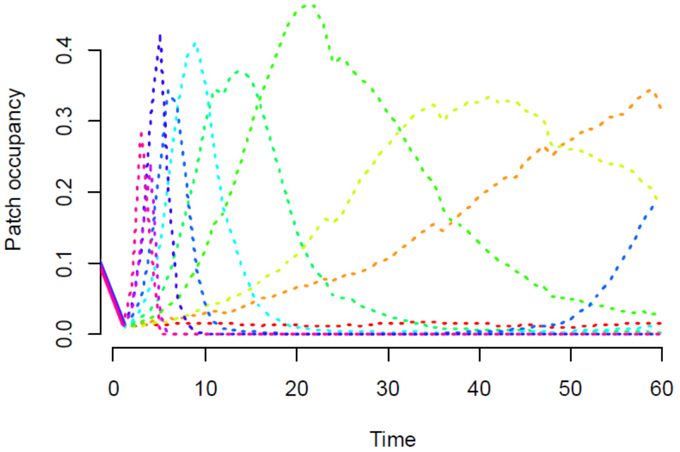

Figure 2: Successional dynamics generated by the ten best competitor / colonizer species.

Best competitor abundance = 20 % ; mortality rate = 10 %, Disturbance frequency = 10 %, disturbance intensity = 10 %

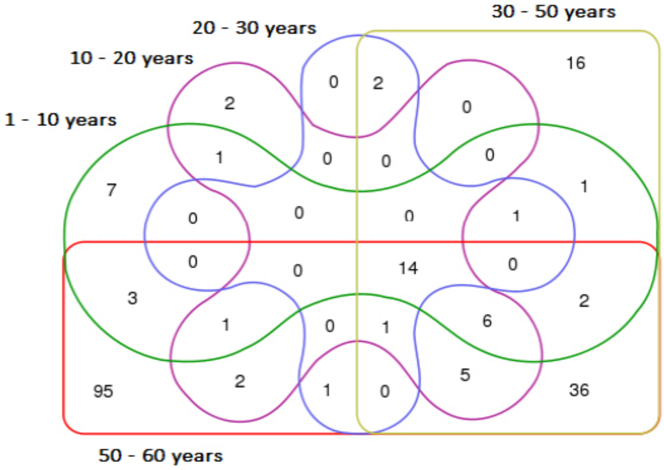

Figure 3: Nonsymmetric Venn diagram showing the number of species shared between the successionalstages

Table I : Characteristics of the flora from differents successional stages

Successional stages (years)	abundance	Richness	Shannon	Simpson	Eveneness
[1 - 10[	476	36	2.94	0.92	0.82
[10 – 20 [	232	32	2.69	0.88	0.78
[20 – 30 [	113	19	2.38	0.85	0.81
[30 - 50[	1117	84	3.21	0.91	0.73
[50 – 60]	2669	166	3.94	0.96	0.77
All habitats	4607	196	3.97	0.96	0.75

Description of the most abundant species

The composition of the five most abundant species changed significantly with successional stages (Table II). Also, these most abundant species have different auto-ecological characters. Three main guild categories were distinguished : non pioneer light demanding (npld), pioneer (pi), and shade tolerant (sb) species.

In the youngest fallow (1 – 10 years), *Acacia mangium* was ranked 1 as this species had the largest total abundance of 85 (18.4 %). *Funtumia elastica* and *Harungana madagascariensis* with respectivelly 13.6 and 9.3 % were fairly abundant. The other species in this chronosequence have relatively low total abundance. In this sequence, only *Funtumia elastica* was non pioneer light demanding (npld). The others were pioneer species.

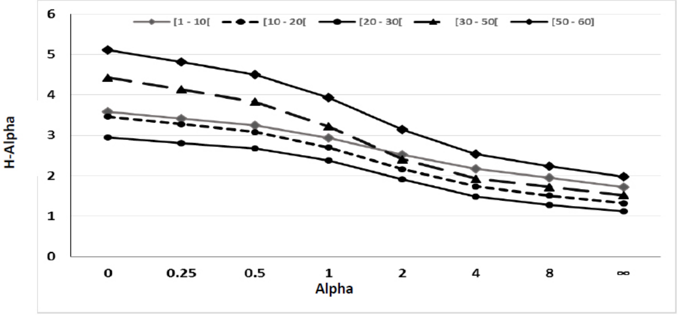

Figure 4 : Comparison of diversity profile for the successional stages

Successional stages (years)	Species	Proportion (%)	Abundance (stems)	Ecologycal guilds	Diaspores type	Phytogeography / Biology
[1 – 10[	*Acacia mangium*	18,4	85	pi	sarcochory	Exotic / mp
	Funtumia elastica	13,6	63	nph	pogonochory	GC / MP
	Harungana madagascariensis	9,3	43	pi	sarcochory	GC / mp
	Macaranga hurifolia	7,6	35	pi	sclerochory	GC / mp
	Anthocleista nobilis	6	28	pi	sarcochory	GCW / mp
[10 - 20[	*Funtumia elastica*	26,7	62	nph	pogonochory	GC / MP
	Anthocleista nobilis	12,9	30	pi	sarcochory	GCW / mp
	Macaranga hurifolia	9,9	23	pi	sclerochory	GC / mp
	Dacryodes klaineana	8,2	19	nph	sarcochory	GC / mP
	Musanga cecropioides	5,2	12	pi	sarcochory	GC / mP
[20 - 30[	*Funtumia elastica*	32,7	37	nph	pogonochory	GC / MP
	Dacryodes klaineana	10,6	12	nph	sarcochory	GC / mP
	Pentadesma butyracea	9,7	11	sb	sarcochory	GC-SZ / MP
	Anthocleista nobilis	8	9	pi	sarcochory	GCW / mp
	Macaranga heudelotii	7,1	8	pi	sclerochory	GC / mp
[30 – 50[	*Funtumia elastica*	21,8	244	nph	pogonochory	GC / MP
	Dacryodes klaineana	16,8	188	nph	sarcochory	GC / mP
	Baphia nitida	6,5	73	sb	ballochory	GC / mp
	Macaranga hurifolia	5	56	pi	sclerochory	GC / mp
	Tarrietia utilis	3,6	40	nph	pterochory	GCW / mP
[50 - 60]	*Tarrietia utilis*	13,9	372	nph	pterochory	GCW / mP
	Baphia nitida	10,2	272	sb	ballochory	GC / mp
	Dacryodes klaineana	5,1	136	nph	sarcochory	GC / mP
	Macaranga hurifolia	4,3	116	pi	sclerochory	GC / mp
	Maesobotrya barteri	3,4	92	sb	sclerochory	GCW / mp

In the fallows of 10 – 20 years old, *Funtumia elastica* was ranked 1 with the largest total abundance (26,7 %) followed by *Anthocleista nobilis* (12,9 %) and *Macaranga hurifolia* (9,9 %). For this sequence, *Funtumia elastica* and other lower abundant species such as *Dacryodes klaineana* were non pioneer light demanding. For these fallows, pioneer species account for more than 50 % of the most abundance species.

In the fallows with 20 – 30 years, *Funtumia elastica, Dacryodes klaineana,* and *Pentadesma butyracea* were the most abundant with respectively 32.7, 10.6 and 9.7 % of total individuals. For this sequence, shade tolerant species become abundant but they proportion was lower than non pioneer light demanding and pioneer species.

In the successional dynamic sequence with 30 – 50 years, the most commun abundant species were *Funtumia elastica (*21.8 % of individuals) and *Dacryodes klaineana* (16.8 % of individuals). For the old forest, the most abundance species were *Tarrietia utilis* (13.9 % of individuals) and *Baphia nitida* (10.2 % of individuals).

For this sequence, non pioneer light demanding and shade tolerant species (*Baphia nitida*) account for more than 50 % of the individuals. For this sequence, the abundance of most pioneer species decreased.

The phytogeographic types of distribution showed more than 60 % of the most abundance species was confined to the Guineo-Congolian (GC) area. Only one species, *Acacia mangeum* is exotic from Africa. Some species such as *Maesobotrya barteri, Tarrietia utilis and Anthocleista nobilis* are endemic to Guineo-Congolian West forest (GCW).

Regardless the diaspore types, sarcochory and sclerochory were well represented and constitutes at least 80 % of the most abundant species in fallows aged from one to thirty years. In more than 30 years old sites, many diaspore types were observed in the same proportion of the most abundant species: sclerochory, ballochory, pterochory and pogonochory.

DISCUSSION

Usually, without human intervention, forest recovery was based on several successionnal stages characterized by some most dominant species or group of species with different auto-ecological characters (Naeem and Wright, 2003). In the South-east of Côte d'Ivoire, the identification of the different sucession stages during forest recovery, has been based on the «multispecies competition-colonization tradeoff» approach. According to this approach, a successionnal stage is established when there is a trade-off between the best colonizer / competitor species during the forest reccovery process. So, each successionnal stage could be characterized by more species coexistence (Lehman and Tilman, 1997). However, this approach has some limits, of which, one has been mainly commented by several authors. For Huston et al. (1988), this forest dynamic model is based on assumptions that don't respect a fundamental biological principle. One of these assumptions is that "all individuals in a population, are identical". That is a paradox because, each individual is unique, and his behavior and physiology result from genetic characteristics modulated by the influence of the environment (Lett, 1999). In other words, parametters (mortality = 10 % and abundance = 20 %) for all species may therefore be the model limits. Shugart and West (1977) recommanded the use of individual models in the population dynamics. In these models, the individual is the basic entity. However, these models called "gap models" (Botkin et al., 1972), are more adpted for small-scale plots such as forest gaps.

For the present study, the "multispecies competition-colonization tradeoff" approach has been based on the existence of a disturbance frequency (20 %) with an intensity of 10 %. This suggested that successionnal processes are not always directional or predictable (Gleason, 1926). There are biological phenomena, which makes this approach one of the best in forest recovery (Shugart 1984; Lett et al., 1999). The assumption that succession is orderly or deterministic and will eventually reach the original forest structure and species composition present before the disturbance, has been so, advoided.

The "multispecies competition-colonization tradeoff" approach permitted to identify five (5) successionnal stages in the South-east of Côte d'Ivoire. Considering the chronosequence, the age class after abandonment of agricultural ([1 – 10 years [, [10 – 20 years [, [20 – 30 years [, and [30 – 60 years [) were more extensive (in the time) than those assumed by some authors on the basis of simple field observation. For example, Kassi et al. (2010) and Mukul and Herbohn (2016) categorized their sites into four different fallow categories: fallows less than 5 years old, hereafter referred to as new, those with 5 - 10 years old, called young fallows, 11-20 year old fallows, considered as middle-aged, and 21-30 year old fallow, considered as oldest. Some other authors such as Richards (1952) have identified three (3) main successionnal stages for west african forest : early stade (1 – 15 years), young secondary forests (15–20 years), and late secondary forest (30–40 years). However, the identified stages in this study were similar to those described by Zanini et al. (2014). These authors have categorized four tree species successional stages according to the age classes proposed by Chazdon (2008) for tropical successional forests : Stage 1 (6 – 10 years), stage 2 (10 – 25 years), stage 3 (26 – 45 years) and stage 4 (over 45 years old). Usualy, this last stade was categorized as old-growth forest. One of the main and common questions about all these study is "what are the diversity levels and the most dominant species at each stage?"

Numerous studies have documented the relationship between forest age and species diversity. At least, during the first 30 years of secondary regrowth, this case study shows that chronosequence data do not correctly reflect true species dynamics. Indeed, over 30 years, there were an increasing of 16 - 95 unique species (19 - 57 %) respectivelly in the secondary forests (30 – 50 years old) and in the old forests. Fallows of [1 – 10 years [have most species rechness and diversity than those of [10 – 20 years [, [20 – 30 years [. Direct comparisons are difficult due to lack of standardization of diversity measures (Chazdon et al., 2007). Saldarriaga et al. (1988) found a positive relationship between stand age and species diversity (Shannon index) in 40 years old secondary forests and old-growth in very small plots. Andel (2001) found higher diversity (Fisher's alpha) in old secondary forests in northwest Guyana than in neighbouring old-growth forests.

For this case study, the decreasing in species richeness and diversity from young fallows (1 – 10 years) to secondary forests (10 – 30 years) can be explained by different human pressures. Indeed, the secondary forests locally called « black forest » according to farmers perception, were under human pressures such as timber logging, hunting, harvesting of toothpicks and of other non timber forest products (NTFPs) harvesting. Effects of all these uncontrolled activities could reduce plant diversity and richness as observed in community forests by Vroh et al. (2015) in the same area. These forests were so regularly disturbed by local people activities. In the old forests including Yapo Protected Forest, the human activities were controlled by SODEFOR (State management structure). Also, in the Natural Voluntary Reserve, these activities were prohibed since 2005. So these two controlled forests have been less harmful to plant species diversity according to all calculated diversity indices.

The results showed also that, for any successionnal stage, one to three most abundant species were pioneer. There were *Acacia mangium, Harungana madagascariensis, Musanga cecropioides*, *Anthocleista nobilis, Macaranga heudelotii,* and *Macaranga hurifolia*. *Acacia mangium* and *Harungana madagascariensis* were among the most abundant species only in the younger fallows (1 - 10 years). This mean that these pioneer species were best colonizer and dominated the community during the first years of regeneration (Chazdon et al., 2007). *Acacia mangium*, an exotic species from Africa, was more used in fallows in order to increase the soil fertilly capacity. It was also presented to be a good fuelwood 5 years after the plantation. This is a relatively short-lived species that does not exceed fifteen years under the climatic conditions of Côte d'Ivoire (Gnahoua and Loupe, 2003). Moreover, this species flowers precociously, and viable seeds can be harvested 24 months after planting (Orwa et al., 2009). The others early colonizer (*Harungana madagascariensis, Musanga cecropioides*, *Anthocleista nobilis, Macaranga heudelotii* and *Macaranga hurifolia*) have been already repported as best colonizer species with the same characters, in the South of Côte d'Ivoire (Alexandre, 1982 ; Khan, 1982). By contrast to *Acacia mangium,* the other pioneer species were among the most dominant in the secondary forests and the old-growth forests. These kind of species have been reported as very long lived pioneer species (Gemerden et al., 2003).

The study showed also that *Funtumia elastica,* commonly named « African wild rubber », a non pioneer light demanding species, was constantly among the most abundant species in all fallows aged from one to 50 years old. This species was reported as a tipical secondary forest species in the South of Côte d'Ivoire and also in other tropical areas (Vroh et al., 2010 ; Verbeeck et al., 2014). *Funtumia elastica* could mark the transition between best colonizers and best competitor species during the successional stages. This species was replaced progressively by two other non pioneer light demanding species (*Dacryodes klaineana* and *Tarrietia utilis*) in the old-growth forests.

In the South-east of Côte d'Ivoire, the abundance of *Tarrietia utilis* and *Dacryodes klaineana* had been demontrated by Corthay (1996) and Vroh et al. (2015). From 20 to 60 years, these two species could be the best competitor species in this area. The gregarious behavior (fruits dispersal no far from mature stems) of *Tarrietia utilis* mentioned by Aké-Assi (2002) in the study area, could be one of the reasons that explain this observation. Trees of *Dacryodes klaineana* may produce a limited number of female flowers, and thus, little fruits (Orwa et al., 2009). These two late successionnal species have the opposite traits (including relatively low fecundity, short dispersal) to those described about early pioneer species.

The first shade tolerant species (*Pentadesma butyracea, Baphia nitida,* and *Maesobotrya barteri*) were among the most abundant species from the secondary forests of 20 – 30 years to the old-growth forests. It is well known that during the tropical forest recovery process, such as the study area, many shade-tolerant climax tree species are capable of survival and growth beneath pioneer trees (Howlett et Davidson, 2003) and may, over time, replace them in a successional sequence (Whitmore, 1998).

The two diaspore types of seed dispersal, sarcochory (fully, partially soft or fleshy diaspore such as those of *Pentadesma butyracea*) and sclerochory (very light diaspore such as those of *Tarrietia utilis* and *Funtumia elastica*) characterized respectively plant species with adaptations for zoochorous and autochorous dispersal (Mosango and Lejoly, 1990). These diaspore types were well represented and constituted at least 80 % of the most abundant species in this case study. This result confirms that the proportion of plant species with adaptations for zoochorous and autochorous dispersal is high among trees and shrubs (Dirzo and Dominguez, 1986) in tropical forest.

CONCLUSION

All results from this study tryed to describe the sucessional process during the forest recovery in the South-east of Côte d'Ivoire. The identified successionnal stages were similar to those described by some authors based on the direct observations on fields. But, these stages were more extensive (in the time) than those assumed by other authors. This means that the sequence and duration of successional phases may vary substantially among tropical forests, depending on the nature of the initializing disturbance and the potential for tree colonization and forest structural development. However, for any author, the forest recovery began with very early pioneer species having short live, followed by the long lived pioneer species, the non pioneer light demanding species, and the shade tolerant species. During the successionnal stages, the richness and diversity have not been influenced by age since abandonment. Clearly, unknown an undetermined factors, other than age, could have had influenced these floristic parameters in the study area. At least, 14 % of forest tree sepcies were surveyed in young fallows. This study showed that farmers practices in Azaguié area, were favorable to the faster regeneration after agricultural abandonment. This rapid forest recovery in the area can provide the availability of farmlands and can be a good opportunity for human pressures reduction on protected forests such as national parcs and reserves. However, will this situation persist for a long time, given the rapid population growth and the growing needs for farmlands in the country?

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