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Mechanisms, Determinants and Model of Early Succession on the Lateritic Plateau of the Sahelian Part of Western Niger

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Abstract

Western Niger lateritic plateaux formally occupied by tiger bush are mainly secondary ecosystems affected by crusting and soil compaction that impedes infiltration and induces intense erosion, which hampered lowlands millet fields. Restoration of these plateaux is essential, but, failure is frequently reported about early species establishment. It's therefore necessary to examine the mechanisms and factors of early plants recovery which are important for vegetation restoration. Vegetation data have been recorded in 31 plots, at four sites with similar environmental characteristics and different land use histories: Unrevegetated area, 1-3-years old revegetated area, 6-years old revegetated area and 14-years old revegetated area. We also measured 16 environmental variables in each plot to examine the driving forces of succession and the vegetation-environment relationships. TWINSPAN results revealed that plant species could be classified into six plant communities representing 4 succession stages. The DCA confirm TWINSPAN classification and indicated two gradients of succession: land condition and successional age. According to the CCA and the Monte Carlo tests, the determinants of succession are succession age, covers of gravel crusts, erosive crusts, barren soil, plants and litter, soil pH, soil contents of organic carbon, organic matter, available phosphorus, calcium, magnesium, total of basic cations and Cation exchange capacity. The chronological changes in plant communities associated with environmental variables contribute to plant assemblage and vegetation development. Since, the environmental variables are able to change with succession age, succession pathways can be divergent, but in the present study it becomes convergent at late stage. As each stage can be structured by more than one plant community, the model of restoring degraded lateritic is closer to alternative stable states model.

Keyworlds: degraded plateau, restoration ecology, biodiversity, models of succession, stochastic dispersal, suitable microsites, succession pathways, alternative stable states

1. Introduction

Succession is the natural development of community or ecosystem. Communities development often follows a typical pattern of continuing species replacement (Wilcox, 1998) wherein initial colonialists, functionally ruderal, initiate autogenic processes favorable to later species establishment (Whisenant, 1999). Investigations into vegetation dynamics have developed several models of ecosystems recovery in response to disturbances included gradual continuum, thresholds and alternative stable states models. The tenor of the first model, assumes system shifts as a linearly changes in vegetation composition, towards an equilibrium single point with perturbations causing shifts along a common trajectory (Clements, 1916; Odum, 1969). Under this framework, changes in abiotic or biotic environmental conditions through restoration were expected to yield proportional, linear changes in plant community structure (James et al., 2013). The second model describes the situation where changes in environmental conditions lead to very little change in species composition or function until a threshold is reached, when a sudden change in composition or function occurs (Suding & Hobbs, 2008). Threshold occurs mainly when a trigger switches the pull of negative feedbacks from one attractor to another attractor. In this condition, restoration treatment focus on removing threshold that restricted vegetation development (Whisenant, 1999). The third model argues the existence of allogenic disturbances that can play a larger role in the behavior of ecosystems than do autogenic processes, such as competition and predation. It's provided several pathways of system dynamic including divergent, cyclic, or arrested trajectories that never arrived at a common state (Hobbs & Suding, 2008). The most fundamental difference between the three models is how they treat alternative stable states (Trumal et al., 2001), although the gradual continuum model predicts a single stable state called climax, the other models predict the existence of many alternative states; which are determined by a combination of factors (e.g. grazing intensity, fire frequency, drought, pollution or nutrient loading) that characterized the environmental condition. The use of these models to guide restoration is becoming an increasingly important tool to repair degraded ecosystems because these models provide temporal frameworks in which to understand aspects of species assembly, community development, biophysical changes of environment, nutrient cycling, etc. It's therefore necessary to understand which of these models can be most closely applied to particular ecosystems to enhance future restoration projects since ecological restoration has become important parts of the sustainable development strategy throughout the world (McClain et al., 2010).

In Western Niger, the lateritic plateaux formally occupied by shrubs bush (locally referred as tiger bush because of its banded pattern with a ratio of vegetation/bare soil cover 1 (Ambouta, 1984; Ichaou, 2000) are mainly secondary ecosystems with high barren surface which included the bare patches in the tiger bush but also, the denuded plateaux, the plateau escarpments, and a few, very poor millet fields on the sandy deposits of the plateaux (d'Herbès & Valentin, 1997). As a whole system, the secondary ecosystems is characterized by its extremely low vegetation cover (less than 5%); and a repeated sequence of impervious crusts, with structural crusts upslope, followed by erosion crusts and gravel crusts midslope and sedimentation crusts downslope (d'Herbès & Valentin, 1997). Such surface features affected by crusting, impede infiltration and induce intense runoff and wind erosion that hampered lowlands millet fields (Casenave and Valentin, 1989; Peugeot et al., 1997). Restoration of these plateaux is essential to increase production of lowland millet fields, for conservation of the biodiversity and to strengthen the provisioning of other essential ecosystem services. This is complicated by several biotic and abiotic thresholds such as crusting, runoff, nutrients and propagules depletions, etc. Restoration of degraded latiritic plateau systems typically centres on planting native plants species in anti-erosive structures such as half-moons, trenches, stone bunds and the like can help overcome these thresholds (Soumana et al., 2014; 2016). Jointly, the nurses plant species and the anti-erosive structures may act to stop the runoff, the depletion of the nutrients and propagules, enhance water infiltration and facilitate the establishment of other woody and understory species, as well as a host of fauna, over the time. This technique has not always been successful and it was often reported failure in early species establishment. Presently, the seriousness of these failures is widely recognized worldwide, many studies are carryied out to enhance success rates of restoration activities. The present study examines the mechanisms and the determinants in changing plant communities and environmental variables on restored laterictic plateau of western Niger. Specifically, the study intendes to identify early succession series of plant communities in restored lateritic plateau, analyses how time and environmental variables influence succession and verify which of them were determinants to plants assembly and replacement, and compares successional models to deduce which of them can be closely applied to enhance restoration efforts of lateritic plateau.

2. Materials and Methods

2.1 Study Area

The study was conducted on the lateritic plateau of Bonkoukou (13°58'484 N, 3°08'896 E, elevation 267 m), in the Sahelian bioclimatic area of the western Niger, at about 140 km from Niamey, the capital city. The climate is typically tropical arid with an annual rainfall of about 560 mm, occurring mainly from June to October; and means minimum and maximum temperatures are 23 and 35 °C, respectively. The high evapotranspiration rates of the Sahelian zone increases water scarcity. The climax vegetation of the plateau of western Niger is patterned by alternatively bands of small trees and shrubs vegetation and bare soils bands (Issa et al., 1999)., from the air the resulting landscape resembles a tiger's fur and is called 'tiger bush' (see Ludwig & Tornway, 1995 ; Valentin et al., 1999; Couteron et al., 2000). The most common woody species of this tiger bush are *Combretum micranthum* and *Guiera senegalensis* (Ambouta 1984; Ichaou, 2000) and the annual species are dominated by *Microchloa indica*, *Cyanotis lanata*, *Zornia glochidiata* and *Schoenefeldia gracilis.* The poor, shallow soils of tiger bush habitats are slightly inclined (slope of a maximum of 1%) and have a high portion of silt, clay and fine particles lying over sedimentary rocks or lateritic crusts (Müller, 2013). Below the sandy-loamy topsoil a coarse-grained sandstone or fine lateritic gravel follows usually in a sandy-loamy matrix.

The restoration areas, formally covered by tiger bush, were eroded long before the onset of the restoration. The study sites that have been restored are part of extremely degraded areas with high compacted soil and physical crusts. The main physical crusts distinguished in the study area are gravel crusts, sedimentation crusts, algal crusts and erosive crusts. A more detailed description of the study areas is given by Issa et al. (1999).

2.2 Restoration Treatments

The restoration treatment of the sites was done by jointly planting tree seedlings and broadcast sowing herbaceous seeds in a water harvesting technique known as a half-moon (Soumana et al., 2016). A half moon is a shallow semi-circular pit that is installed on sloping land: the pit increases in depth from the up-slope to the down-slope side thereby forming a semi-circular micro-catchment pit to capture runoff water, topsoil, litter and seeds. The half moons were installed on compacted and barren soil dominated by gravel, erosive and algal crusts, with a vegetation cover less than 5%, where erosion is very active and infiltration is very low (Casenave & Valentin, 1989). The dimension of each half moon was 3 m in diameter on the up-slope side, 2 m in length from the up-slope to lower-slope sides, with a maximum depth of 0.25 m on the down-slope side. One seedling of tree species (*Bauhinia rufescens*, *Acacia senegal, Acacia seyal*) were planted in each half moon, and seeds of two herbaceous species (*Schyzachyrium exile*, *Penicetum pedicellatum* and *Zornia glochidiata*) were broadcast-sown in the half moons. These species were selected by the local community because they are well adapted to the area, can rapidly restore degraded lands and provide socio-economic benefits. These treatments have been done to accelerate the rate of plants succession.

2.3 Data Collection

To analyze the composition and the structure of the plant communities of each succession stage, vegetation and sites characteristics were recorded in rectangular plots (50 m by 20 m) that were randomly placed in four sites with similar environmental characteristics and different land use histories: (i) Unrevegetated area and (ii) 1-3-years old revegetated area, (iii) 6-years old revegetated area (iv) 14-years old revegetated area. Within each plot, average height of herbaceous plant species was recorded, and relative cover of erosive crust, gravel crust, bare ground, rock, litter, and vascular plants cover were assessed using the Braun-Blanquet (1932) cover-abundance scale (1 = 0.5; 2 = 3; 3 = 15; 4 = 37.5; 5 = 62.5; 6 = 87.5). Soil samples were randomly collected from 5 points in each plot using a 5 cm diameter soil auger to a depth of 20 cm after removing surface litter. A composite soil sample of about 1 kg from each plot was collected, air-dried and sieved for analysis of soil chemical and physical characteristics (Laboratoire de sol, Faculté d'Agronomie, Université Abdou Moumouni de Niamey).These data were collected at the end of September 2014 which coincides with the ending of the rainfall season and the beginning of the dry season in the Sahel; at this moment plant composition and cover can be underestimated (Saadou, 1990). Nomenclature adopted for plants is that of Lebrun & Stork (1997). Seed and fruit dispersal types were evaluated according to the scheme of Dansereau & Lems (1957) which distinguishes dispersal types primarily by morphology of the diaspore.Plants life forms were determined according to Raunkiaer (1934) classification which emphaizes the position of the perennating or renewal buds of plants (Stanley, 1950).

2.4 Data Analysis

First, Two-way Indicator-Species Analysis (TWINSPAN; Hill 1979) based on the plants presence-absence was used to classify the succession stage of the plants communities. Second, Detrended Correspondence Analysis (DCA, Hill & Gauch, 1980) was used to analyze relationship between succession stages and to observe patterns of vegetation along the restoration ages. Third, Multi-Response Permutation Procedures test (MRPP: McCune & Grace, 2002) was used to test the difference in species composition between succession stages and the heterogeneity within each stage. The data matrix for MRPP was the squared Euclidean distance between each pair of the 34 plots based on relative abundance of the 114 species. MRPP is a non-parametric multivariate procedure that tests between species composition of two or more *a priori* sites. MRPP provides three values: A (change-corrected within site agreement) tests the homogeneity within site; when all of the observations within groups are identical, then the observed delta = 0 and A = 1; T (the difference between the observed and expected deltas) tests the difference between two or more groups (sites), and p-value tests the difference between groups (stages). Fourth, the most frequent and dominant species of each succession stages were identified by subjecting the matrix of 34 plots and 114 species to Indicator Species Analysis (ISA; Dufrene & Legendre, 1997; McCune & Grace, 2002). ISA has the advantage of combining both the relative frequency (RF) and relative abundance (RA) for calculating the Indicator Value (IV) of each specie, and the significance is tested by the Monte Carlo test. All species with a probability less than 0.05 were accepted as more frequent and abundant species. The Indicator Value was calculated using the following formula: $IV_{kj} = RA_{kj} \times RF_{kj} \times 100$, where RA is the relative abundance of a given species j in a given site type k and RF is the proportional frequency of species j in site type k (i.e., the proportion of plots in each site type with species j). Values of IV ranged from 0 to 100 (perfect indication). A perfect indicator value means that a given species occurs only in a given site type and are always in that site type. Fith, Canonical Correspondence Analysis (CCA; Braak, 1986) was implemented with Monte Carlo permutation test to analyze the relationship between the pattern of vegetation communities and the environmental variables. Monte

Carlo permutation provides P-values that tested the statistical significance of each environmental variable. Finally, differences in soil chemical characteristics between succession stages fields were analyzed using Tukey's hsd post hoc tests after one-way Analysis of Variance (ANOVA). Before running the ANOVA test, the normalities of the soil variables were tested by using the test of Kolmogorov-Smirnov.

Minitab version 16 (Dytham, 2011) was used for the test of Kolmogorov-Smirnov and one way ANOVA with Tukey's post hoc tests. TWINSPAN, MRPP and ISA were done using PC-ORD Version 5 (McCune & Grace, 2002). CANOCO version 4.5 (Ter Braak & Smilauer, 1998) was used for DCA and CCA.

3. Results

3.1 Succession Stages

Globally, 114 plants species were recorded into 34 plots. After restoration treatments, species richness changes and increases rapidly during the first three years, peaked at the three years and decreased with the restoration ages, at the same time as, plants cover increased (Figure 3). TWINSPAN classified the matrix of 34 plots and 114 plants species into six (6) communities, representing four (4) temporal succession stages (Figure 1) that are structured by different plants species (Table 1): stage I = untreated site with one plants community, stage II = one to tree years old restoration sites with one plants community, stage III = tree to six years old restoration sites with two plants communities (*Aristida adscensionis* L.- *Cenchrus* prieurii (Kunth.) Maire community and *Acacia Senegal*- *Stylosanthes erecta* P. Beauv. Community, and stage IV with two plants communities (*A. nilotica*- *Microchloa indica* community and *Ziziphus mauritiana*- *Eragrostis pilosa* Community). MRPP based on plants and environmental variables revealed high differences ($P < 0.001$; $A = 0.47$; T statistics = -14.43) of plants composition between the four successional stages and between the six plants communities (Table 2). Each paire-wise comparison by MRPP showed that successional stages differed significantly. The small difference between the excepted (0.50) and observed delta (0.26) values confirms the strong variation in species composition between stages. The lower value of A (0.47) reveals significant variations in species composition between plots of same age, reflecting the high differences between the six plants communities.

Table 2. Summary of the Multi-response Permutation Procedure (MRPP) statistics of the successional stages on the restored lateritics plateau of Western Niger. Results are given for the MRPP and the multiple pairwise comparisons of the squared Euclidean distance. A = change-corrected withingroup agreement; T = difference between the observed and expected deltas

Compared stages	T	A	p	MRPP test
Stage 1 vs. Stage 2	-8.21	0.39	0.00	Observed delta = 0.26
Stage 1 vs. Stage 3	-9.57	0.39	0.00	Excepted delta = 0.50
Stage 1 vs. Stage 4	-7.07	0.44	0.00	T = -14.43
Stage 2 vs. Stage 3	-6.00	0.17	0.00	A= 0.47
Satge 2 vs. Stage 4	-9.08	0.44	0.00	P < 0.00
Stage 3 vs. Stage 4	-4.58	0.16	0.00	

Stage I: (unrevegetated sites, Community I): the vegetation cover and plants composition were very low respectively 5.5±0.4% and 32 species compared to the restored sites (Figure 3). The unrevegetated sites are practically barren with compacted soil and several physical crusts, favorable to active erosion and seeds depletion. In this condition, seeds germination and development are precarious. Plant composition is typical of late successional stage with remanent plant species like *Boscia senegalensis* (Pers.) Lam. Ex Poir., *Boscia angustifolia* A. Rich. and *Maerua crassifolia* Forsk (phanerophytes) and *Stylochiton hypogaeus* Lepr. (therophyte) (Table 1).

Stage II: 1 to 3 years after restoration treatments (Community II), the plants cover is low (19.33±4.56%) and the plants composition higher compared to the old restored areas (89 species). Among the 89 plants species recorded, 33 have their greatest relative abundance and frequency at this stage which are mainly ruderals. These plants include *Aristida funiculata* Trin. Et Rupr., *Aristida sieberiana* Trin*., Panicum subalbidum* Kunth*. Pennisetum pedicellatum* Trin. (gramineous), *Amaranthus spinosus* L., *Tephrosia linearis* (Willd.) Pers*.*, *Jacquemontia tamnifolia* (L.) Griseb. (phorbes), etc (Table 1).

Stage III: 3 to 6 years after the revegetation, the average plants cover and the plants composition are 35.18±13.06% and 83 plants species, among 40 species have the highest abundance and frequency scores at this stage (table1). These species include phanerophytes (*Acacia seyal* Del., *A. laeta* R.Br. Ex Benth., *A. senegal* (L.) Willd., *Ziziphus mauritiana* Lam.) and therophytes (*Zornia glochidiata* Reichb. Ex DC., *Schizachyrium exile* (Hochst.) Pilger, *Schoenefeldia gracilis* Kunth. Etc.). The phanerophytes become more dominant and the plants richness lower compared to the previous stage. This stage includes two plants communities: *Aristida adscensionis* L.- *Cenchrus* prieurii (Kunth.) Maire. (Community III) occurred commonly at the three and six years old restored sites, it's structured by *Calotropis procera* (Ait.) R. Br., *Pandiaka angustifolia* (Vahl) Hepper., *Schoenefeldia gracilis* Kunth. Lam. The second plants community is *Acacia Senegal*- *Stylosanthes erecta* P. Beauv. Community (IV) located only in the six years old restored sites, structured by *Pupalia lappacea* (L.) Juss., *Peristrophe bicalyculata* (Retz.) Nees., *Monechma ciliatum* (Jacq.) Miln.-Red., etc. These communities can be considered as alternative stages among the multiple stages that can be this stage.

Stage IV: Six 6 to 14 years after revegetation, the plants cover average and the plants composition are 44±7% and 83 plant species, among these species, 72 have the greatest abundance and frequency. This stage can be divided into two (2) plants communities: *Acacia nilotica*- *Microchloa indica* community at the beginning of the stage, structured by *Bidens biternata* (Lour.) Merrill., *Ipomoea vagans* Bak. et Sherff, *Faidherbia albida* (Del.) A. Chev., etc. (Community V, see Table 1) located commonly at the six and the 14 years restored sites; At the end of the stage, the community composition and the structure changed and it's become *Ziziphus mauritiana*- *Eragrostis pilosa* Community (VI) dominated by *Panicum laetum* Kunth., *Cenchrus biflorus* Roxb., *Alysicarpus ovalifolius* (Schum. & Thonn.) J. Leon., etc. (Table 1) which structured the community. This community is located only in the 14 years restored sites.

Table 1. Family, life form (LF), Dispersal type (DP), Relative abundance (RA), frequency (RF), indicator value (IV), and statistical significance of indicator value (P) of plant species in Successional stage (SS), revegetated and unrevgetated sites and plants communities

Indicator species	Families	LF	DP	SS	Occured sites	Plant communities	RA	RF	IV	P-values
Boscia senegalensis (Pers.) Lam. Ex Poir.	Capparaceae	McPh	Sarco	I	Unrevegetated sites	BOSN-MACR	52	67	34	0.08
Boscia angustifolia A. Rich.	Capparaceae	McPh	Sarco	I	Unrevegetated sites	BOSN-MACR	47	67	31	0.12
Maerua crassifolia Forsk.	Capparaceae	McPh	Sarco	I	Unrevegetated sites	BOSN-MACR	47	67	31	0.11
Stylochiton hypogaeus Lepr.	Araceae	Th	Sarco	I	Unrevegetated sites	BOSN-MACR	100	17	17	0.52
Dactyloctenium aegyptium (L.) Willd.	Poaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	57	100	57	0.00
Panicum subalbidum Kunth.	Poaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	100	75	75	0.00
Jacquemontia tamnifolia (L.) Griseb.	Convolvulaceae	LTh	Sclero	II	1-3 years revegetated	DAAE-PASU	58	88	51	0.00
Digitaria horizontalis Willd.	Poaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	35	100	35	0.00
Polycarpea corymbosa Lam.	Caryophyllaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	67	75	50	0.01
Mollugo nudicaulis Lam.	Molluginaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	29	100	29	0.01
Sesbania pachycarpa DC.	Leguminosae-Papilionoideae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	100	13	13	0.02
Pennisetum pedicellatum Trin.	Poaceae	Th	Pogo	II	1-3 years revegetated	DAAE-PASU	32	100	32	0.03
Cleome monophylla L.	Capparaceae	Th	Auxo	II	1-3 years revegetated	DAAE-PASU	63	63	39	0.04
Alternanthera nodiflora R. Br.	Amaranthaceae	Gr	Sclero	II	1-3 years revegetated	DAAE-PASU	56	63	35	0.07
Aristida sieberiana Trin.	Poaceae	Th	Sarco	II	1-3 years revegetated	DAAE-PASU	57	50	29	0.07
Aristida funiculata Trin. Et Rupr.	Poaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	100	38	38	0.09
Waltheria indica L.	Sterculiaceae	CH	Desmo	II	1-3 years revegetated	DAAE-PASU	19	100	19	0.10
Chrozophora brocchiana Vis.	Euphorbiaceae	NnPh	Pogo	II	1-3 years revegetated	DAAE-PASU	47	63	29	0.12
Spermacoce radiata (DC.) Hiern.	Rubiaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	44	50	22	0.14
Commelina forskoalei Vahl.	Commelinaceae	Th	Auxo	II	1-3 years revegetated	DAAE-PASU	100	25	25	0.15
Amaranthus spinosus L.	Amaranthaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	100	25	25	0.16
Spermacoce chaetocephala DC	Rubiaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	30	88	26	0.22
Corchorus olitorius L.	Tiliaceae	Th	Sarco	II	1-3 years revegetated	DAAE-PASU	67	25	17	0.25
Mitracarpus villosus (Sw.) DC.	Rubiaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	36	63	22	0.36
Tephrosia linearis (Willd.) Pers.	Leguminosae-Papilionoideae	Th	Ballo	II	1-3 years revegetated	DAAE-PASU	80	50	40	0.50
Maerua angolensis DC.	Capparaceae	McPh	Sarco	II	1-3 years revegetated	DAAE-PASU	50	25	13	0.56
Acacia holosericea	Leguminosae-Mimosoideae	McPh	Sclero	II	1-3 years revegetated	DAAE-PASU	40	25	10	0.83

Ipomoea vagans Bak.	Convolvulaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	22	63	14	0.94
Citrillus colocynthis (L.) Schrad.	Cucurbitaceae	LCH	Sarco	II	1-3 years revegetated	DAAE-PASU	100	13	13	1.00
Ceratotheca sesamoides Endl.	Pedaliaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	100	13	13	1.00
Cymbopogon schoenantus (L.) Spreng.	Poaceae	H	Sclero	II	1-3 years revegetated	DAAE-PASU	100	13	13	1.00
Digitaria longiflora (Retz.) Pers.	Poaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	50	13	6	1.00
Phyllanthus pentandrus Schum.&Thonn.	Euphorbiaceae	Th	Sarco	II	1-3 years revegetated	DAAE-PASU	100	13	13	1.00
Setaria pallide fusca (Schumach.) Stapf.	Poaceae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	50	13	6	1.00
Crotalaria senegalensis (Pers.) Bak. ex. DC.	Leguminosae-Papilionoideae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	75	50	38	0,03
Indigofera dendroides Jacq.	Leguminosae-Papilionoideae	Th	Sclero	II	1-3 years revegetated	DAAE-PASU	50	38	19	0,45
Eragrostis tenella (L.) Roem. et Schult.	Poaceae	Th	Sclero	III	3-6 years revegetated	ERTE-CEPR	31	100	31	0.03
Solanum incanum L.	Solanaceae	Th	Sarco	III	3-6 years revegetated	ERTE-CEPR	100	50	50	0.03
Cucumis melo Naud.	Cucurbitaceae	LTh	Sarco	III	3-6 years revegetated	ERTE-CEPR	67	50	33	0.07
Cenchrus prieurii (Kunth.) Maire.	Poaceae	Th	Desmo	III	3-6 years revegetated	ERTE-CEPR	67	50	33	0.07
Calotropis procera (Ait.) R. Br.	Asclepiadaceae	McPh	Pogo	III	3-6 years revegetated	ERTE-CEPR	57	50	29	0.09
Schoenefeldia gracilis Kunth.	Poaceae	Th	Sclero	III	3-6 years revegetated	ERTE-CEPR	28	100	28	0.10
Pergularia tomentosa L.	Asclepiadaceae	NnPh	Pogo	III	3-6 years revegetated	ERTE-CEPR	57	50	29	0.16
Pandiaka angustifolia (Vahl) Hepper.	Amaranthaceae	Th	Sclero	III	3-6 years revegetated	ERTE-CEPR	28	100	28	0.17
Sesamum alatum Thon.	Pedaliaceae	Th	Sclero	III	3-6 years revegetated	ERTE-CEPR	46	50	23	0.20
Bauhinia rufescens Lam.	Leguminosae-Caesalpinioideae	McPh	Sclero	III	3-6 years revegetated	ERTE-CEPR	32	75	24	0.28
Zornia glochidiata Reichb. Ex DC.	Leguminosae-Papilionoideae	Th	Desmo	III	3-6 years revegetated	ERTE-CEPR	24	100	24	0.31
Schizachyrium exile (Hochst.) Pilger.	Poaceae	Th	Sclero	III	3-6 years revegetated	ERTE-CEPR	24	100	24	0.32
Bidens biternata (Lour.) Merrill. et Sherff.	Asteraceae = Compositae	Th	Desmo	III	3-6 years revegetated	ERTE-CEPR	100	25	25	0.35
Cleome viscosa L.	Capparaceae	Th	Auxo	III	3-6 years revegetated	ERTE-CEPR	67	25	17	0.49
Cucumis prophetarum L.	Cucurbitaceae	LNnPh	Sarco	III	3-6 years revegetated	ERTE-CEPR	67	25	17	0.50
Spermacoce radiata (DC.) Hiern.	Rubiaceae	Th	Sclero	III	3-6 years revegetated	ERTE-CEPR	67	25	17	0.50
Corchorus tridens L.	Tiliaceae	Th	Sclero	III	3-6 years revegetated	ERTE-CEPR	50	25	13	0.54
Andropogon gayanus Kunth.	Poaceae	H	Sclero	III	3-6 years revegetated	ERTE-CEPR	27	75	20	0.54
Boerhavia erecta L.	Nyctaginaceae	Th	Sclero	III	3-6 years revegetated	ERTE-CEPR	50	25	13	0.56
Ipomoea coptica (L.) Roth. ex. Roem. et Schult.	Convolvulaceae	LTh	Sclero	III	3-6 years revegetated	ERTE-CEPR	50	25	13	0.56
Acacia senegal (L.) Willd.	Leguminosae-Mimosoideae	McPh	Sclero	III	3-6 years revegetated	ERTE-CEPR	19	100	19	0.67
Commiphora africana (A.Rich.) Engl.	Burseraceae	McPh	Sclero	III	3-6 years revegetated	ERTE-CEPR	38	25	9	0.75
Triumfetta pentandra A. Rich.	Tiliaceae	Th	Sarco	III	3-6 years revegetated	ERTE-CEPR	29	25	7	0.83
Acacia laeta R.Br. Ex Benth.	Leguminosae-Mimosoideae	McPh	Sclero	III	3-6 years revegetated	ERTE-CEPR	27	50	13	0.86
Pupalia lappacea (L.) Juss.	Amaranthaceae	Th	Desmo	III	6 years revegetated	ACTO-STER	57	100	57	0.00
Stylosanthes erecta P. Beauv.	Leguminosae-Papilionoideae	Th	Desmo	III	6 years revegetated	ACTO-STER	50	100	50	0.00
Peristrophe bicalyculata (Retz.) Nees.	Acanthaceae	Th	Pogo	III	6 years revegetated	ACTO-STER	86	75	64	0.00
Acacia tortilis (forsk.) Hayne	Leguminosae-Mimosoideae	McPh	Sarco	III	6 years revegetated	ACTO-STER	37	100	37	0.00
Monechma ciliatum (Jacq.) Miln.-Red.	Acanthaceae	Th	Desmo	III	6 years revegetated	ACTO-STER	32	100	32	0.01
Cassia mimosoides L.	Leguminosae-Caesalpinioideae	Th	Ballo	III	6 years revegetated	ACTO-STER	32	100	32	0.03
Pavonia triloba Guill. Et Perr.	Malvaceae	Th	Sclero	III	6 years revegetated	ACTO-STER	100	50	50	0.03
Cienfuegosia digitata Cav.	Malvaceae	Th	Pogo	III	6 years revegetated	ACTO-STER	80	50	40	0.05
Achyrantes aspera L.	Acanthaceae	Th	Desmo	III	6 years revegetated	ACTO-STER	33	100	33	0.07
Merremia pinnata (Choisy.) f.	Convolvulaceae	LTh	Sclero	III	6 years revegetated	ACTO-STER	38	75	28	0.07
Hibiscus asper Hook. f.	Malvaceae	Th	Sclero	III	6 years revegetated	ACTO-STER	55	50	27	0.19
Prosopis juliflora (Sw.) DC.	Leguminosae-Mimosoideae	McPh	Sclero	III	6 years revegetated	ACTO-STER	100	25	25	0.3487
Sclerocarya birrea (A. Rich.) Hochst.	Anacardiaceae	MgPh	Sarco	III	6 years revegetated	ACTO-STER	100	25	25	0.3593
Combretum glutinosum Perr, ex DC.	Combretaceae	McPh	Ptero	III	6 years revegetated	ACTO-STER	67	25	17	0.4947
Tephrosia purpurea (L.) Pers.	Leguminosae-Papilionoideae	Th	Sclero	III	6 years revegetated	ACTO-STER	67	25	17	0.5015
Indigofera astragalina DC.	Leguminosae-Papilionoideae	Th	Ballo	III	6 years revegetated	ACTO-STER	31	50	15	0.6345
Microchloa indica (L. f.) P. Beauv.	Poaceae	Th	Sclero	VI	6-14 years revegetated	ACNI-MIIN	64	88	56	0.004
Bidens biternata (Lour.) Merrill. et Sherff	Asteraceae = Compositae	Th	Desmo	VI	6-14 years revegetated	ACNI-MIIN	100	50	50	0.0136
Ipomoea vagans Bak.	Convolvulaceae	LTh	Sclero	VI	6-14 years revegetated	ACNI-MIIN	67	50	33	0.045
Acacia nilotica (L.) Willd.	Leguminosae-Mimosoideae	McPh	Sclero	VI	6-14 years revegetated	ACNI-MIIN	56	63	35	0.073
Spermacoce ruelliae DC.	Rubiaceae	Th	Sclero	VI	6-14 years revegetated	ACNI-MIIN	100	38	38	0.09

Faidherbia albida (Del.) A. Chev.	Leguminosae-Mimosoideae	McPh	Sarco	VI	6-14 years revegetated	ACNI-MIIN	100	38	38	0.1004
Dipcadi taccazeanum (Hochst. Ex A. Rich.) Bak.	Liliaceae	Ge	Sclero	VI	6-14 years revegetated	ACNI-MIIN	48	50	24	0.12
Eragrostis pilosa (L.) P. Beauv.	Poaceae	Th	Sclero	VI	6-14 years revegetated	ACNI-MIIN	100	25	25	0.1698
Cassia sieberiana DC.	Leguminosae-Caesalpinioideae	McPh	Ballo	VI	6-14 years revegetated	ACNI-MIIN	67	25	17	0.2625
Indigofera hirsuta Linn.	Leguminosae-Papilionoideae	Th	Sclero	VI	6-14 years revegetated	ACNI-MIIN	67	25	17	0.2647
Citrillus lanatus (Thunb.) Matsumara et Naka	Cucurbitaceae	LTh	Sarco	VI	6-14 years revegetated	ACNI-MIIN	67	25	17	0.2657
Balanites aegyptiaca (L.) Del.	Balanitaceae	McPh	Sarco	VI	6-14 years revegetated	ACNI-MIIN	36	63	22	0.3549
Pancratium trianthum Herb.	Amaryllidaceae	Gb	Sclero	VI	6-14 years revegetated	ACNI-MIIN	27	50	14	0.5855
Indigofera bracteolata DC.	Leguminosae-Papilionoideae	Th	Ballo	VI	6-14 years revegetated	ACNI-MIIN	38	25	9	0.7483
Ipomoea eriocarpa R.Br.	Convolvulaceae	LTh	Sclero	VI	6-14 years revegetated	ACNI-MIIN	26	63	16	0.7628
Sida ovata Forsk.	Malvaceae	CH	Desmo	VI	6-14 years revegetated	ACNI-MIIN	23	63	14	0.9126
Commelina benghalensis L.	Commelinaceae	Th	Auxo	VI	6-14 years revegetated	ACNI-MIIN	100	13	13	1
Dicoma tomentosa Cass.	Asteraceae = Compositae	Th	Desmo	VI	6-14 years revegetated	ACNI-MIIN	100	13	13	1
Diheteropogon hagerupii Hitch.	Poaceae	Th	Sclero	VI	6-14 years revegetated	ACNI-MIIN	100	13	13	1
Eragrostis pilosa (L.) P. Beauv.	Poaceae	Th	Sclero	VI	6-14 years revegetated	ACNI-MIIN	100	13	13	1
Euphorbia convolvuloides Hochst. ex Benth.	Euphorbiaceae	Th	Sclero	VI	6-14 years revegetated	ACNI-MIIN	100	13	13	1
Eragrostis tremula Steud.	Poaceae	Th	Sclero	VI	14 years revegetated	ZIMA-ERTR	39	100	39	0.0036
Panicum laetum Kunth.	Poaceae	Th	Sclero	VI	14 years revegetated	ZIMA-ERTR	31	100	31	0.0132
Cenchrus biflorus Roxb.	Poaceae	Th	Desmo	VI	14 years revegetated	ZIMA-ERTR	33	100	33	0.0154
Ziziphus mauritiana Lam.	Rhamnaceae	McPh	Sarco	VI	14 years revegetated	ZIMA-ERTR	25	100	25	0.023
Alysicarpus ovalifolius (Schum. & Thonn.) J. Leon	Leguminosae-Papilionoideae	Th	Sclero	VI	14 years revegetated	ZIMA-ERTR	34	100	34	0.0462
Cyperus iria L.	Cyperaceae	Th	Sclero	VI	14 years revegetated	ZIMA-ERTR	80	50	40	0.055
Indigofera colutea (Burm.f.) Merril. Phill.	Leguminosae-Papilionoideae	Th	Ballo	VI	14 years revegetated	ZIMA-ERTR	31	100	31	0.0836
Piliostigma reticulatum (DC.) Hochst.	Leguminosae-Caesalpinioideae	McPh	Sclero	VI	14 years revegetated	ZIMA-ERTR	26	100	26	0.2861
Aristida adscensionis L.	Poaceae	Th	Sclero	VI	14 years revegetated	ZIMA-ERTR	23	100	23	0.2881
Acacia seyal Del.	Leguminosae-Mimosoideae	McPh	Sclero	VI	14 years revegetated	ZIMA-ERTR	100	25	25	0.3453
Leucas martinicensis (Jacq.) R. Br.	Labiatae = Lamiaceae	Th	Sclero	VI	14 years revegetated	ZIMA-ERTR	50	25	13	0.5475
Chloris pilosa Schum.	Poaceae	Th	Sclero	VI	14 years revegetated	ZIMA-ERTR	50	25	13	0.5639
Elionurus elegans Kunth.	Poaceae	Th	Sclero	VI	14 years revegetated	ZIMA-ERTR	50	25	13	0.5753
Evolvulus alsinoides (L.) L.	Convolvulaceae	Th	Sclero	VI	14 years revegetated	ZIMA-ERTR	22	100	22	0.7337
Guiera senegalensis J.F. Gmel.	Combretaceae	McPh	Pogo	VI	14 years revegetated	ZIMA-ERTR	19	100	19	0.8502
Combretum micranthum G.Don.	Combretaceae	McPh	Ptero	VI	14 years revegetated	ZIMA-ERTR	20	75	15	0.9592

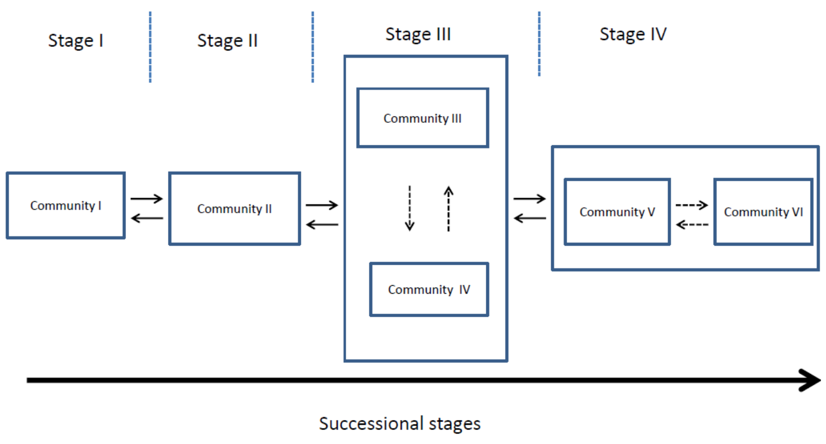

Figure 2. Model of restoring plant communities on degraded lateritic plateau in western Niger. Dashed arrows depict reversible transition between plant communities (states) within stage and solid arrows depict reversible transition among successional stages

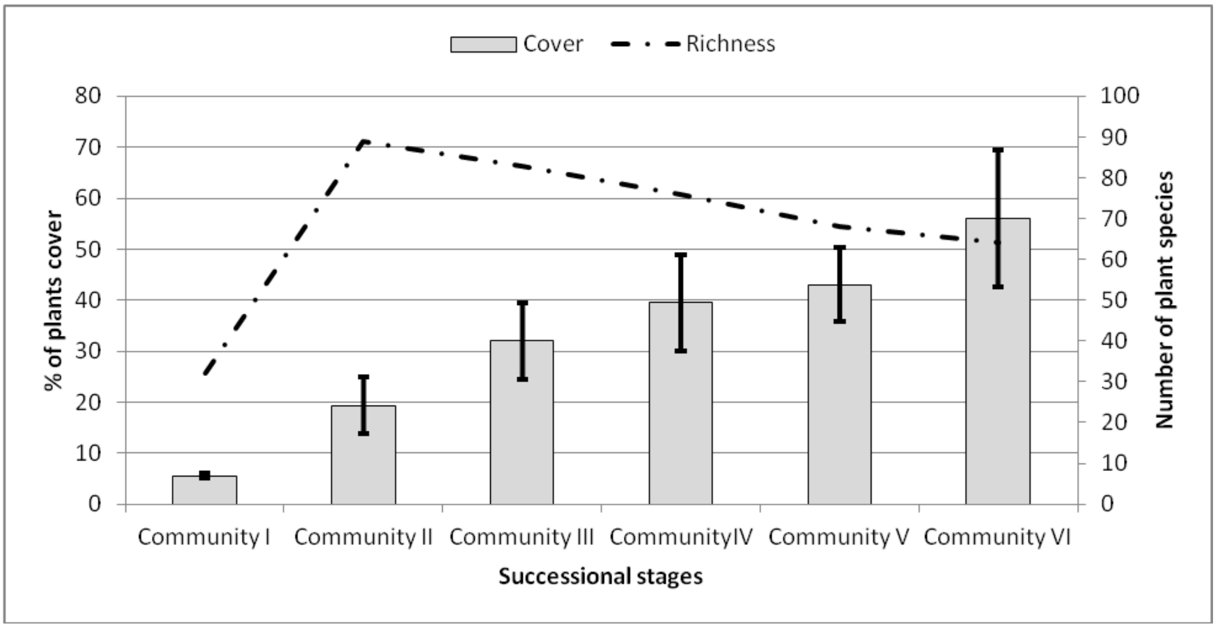

Figure 3. Change in successional stages of plants cover and composition

Raunkiaer (1934) lifeforms: Ch = Chamaephyte (small shrubs and herbaceous perennials with exposed buds less than 50 cm above ground level), H = Hemycryptophyte (small shrubs and herbaceous perennials with exposed buds at ground level), McPh = Microphanerophyte (trees with exposed buds 2 to 8 m above ground level), MgPh = Megaphanerophyte (trees with exposed buds at least 30 m above ground level), NnPh = Nanophanerophyte (trees with buds 0.25 to 2 m above ground evel), Th = Therophyte (annual plants). The dispersal types are Auxo: auxochore, Ptero: pterochore, Pogo: pogonochore, Desmo: desmochore, Sarco: sarcochore, Sporo: sporochore, Sclero: sclerochore, Ballo: ballochore. Plants communities are : BOSN-MACR = *Boscia senegalensis-Maerua crassifolia* community, DAAE-PASU= *Dactyloctenium aegyptium-Panicum subalbidum* community, ERTE-CEPR = *Aristida adscensionis - Cenchrus prieurii* community, ACTO-STER= *Acacia Senegal-Stylosanthes erecta* community, ACNI-MIIN =*Acacia- nilotica- Microchloa indica* community, ZIMA-ERTR = *Ziziphus mauritiana- Eragrostis pilosa* community

3.2 Driving Factors of Species Assembly and Replacement

Ordination axis 1 and 2 of the DCA which cumulatively total 0.71 and 14% of the eigenvalue and the variance, explain more the distribution of the information in the diagram (Figure 4). In the graph, axis 1 (eigenvalue = 0.43; variance = 8%; Lengths of gradient = 2.48) was negatively linked with plots from 1-3 years old restored sites, inversely with plots from 6-14 restored sites and between them, plots from 3-6 years old restored. On this axis, from left to right, plants communities change structure, composition and richness as soon as restoration ages become longer. Axis 1 reveals succession of plants communities with restoration ages. Axis 2 (Eigenvalue = 0.28; variance = 6%; Lengths of gradient = 2.33) separate at upper storey, plots from unrevegetated sites with compacted soil, physical crusts, active erosion feature, etc. and at its lower storey, plots from revegetated sites with anti-erosive catchments and plantation. Axis 2 reflects land conditions (disturbance level and moisture condition) gradient. Changes in land conditions due to treatment with anti-erosive catchment and plantation induce differences between revegetated and unrevegetated sites. Therefore, land conditions and time seem to be the detertminants of plants recovery.

3.3 Changes of Species Traits Over Successional Course

After the restoration treatments there are temporal changes of plants composition, richness and plants cover (Table 1, Figure 4). Fluctuation of plants composition induces changes in plants life traits and communities structure. Moreover, successional stages life forms and dispersal types spectrums (raw and weighted) changed differently with restoration treatments and ages (Figures 5, 6, 7, 8). Globally, at all the sucessional stages, the most abundant life forms are the Therophytes, followed by the Phanerophytes, the other life forms are less abundant (Figure 5). Similar trends were observed in the weighted life forms spectrum with the unrevegetated site (community I) and the early stages of restoration (communities II and III) (Figure 6). At the intermediate stages (Communities IV and V) and at the late stage, the weighted spectrum is successively dominated by the Phanerophytes and the Therophytes. However, after restoration treatments, the proportion number of therophytes increases rapidly then decreases with restoration ages while the number and the cover of phanerophytes increase. As for the dispersal types, the raw spectrum for the successional stages is characterized by the dominancy of sclerochores excepted the stage II (community II) which is dominated by the sarcochores (Figure 7). But the weighted spectrum is successively dominated by the sclerochores, pogochores and the sarcochores with the unrevegetated site; by the sarcochores, the desmochores and the sclerochores with the young revegetated sites (early successional stage: community II), by pogochores, the sclerochores and the desmochores with the intermediate revegetated sites (intermediate successional stage: communities III and IV); and by the sclerochores, the desmochores and the sarcochores with the old revegetated sites (late successional stage: communities V, VI) (Figure 8).

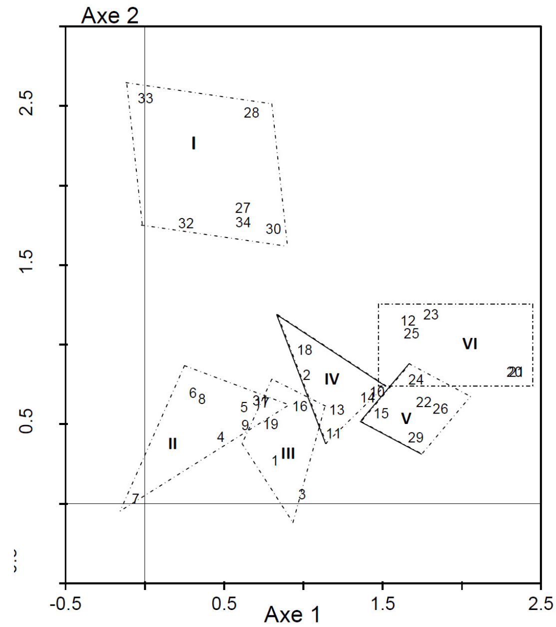

Figure 4. DCA ordination result showing the six community types derived from TWINSPAN analysis: I= *Boscia senegalensis-Maerua crassifolia* community, II = *Dactyloctenium aegyptium-Panicum subalbidum* community, III = *Aristida adscensionis - Cenchrus prieurii* community , IV = *Acacia Senegal- Stylosanthes erecta* community, V =*Acacia- nilotica- Microchloa indica* community, VI = *Ziziphus mauritiana- Eragrostis pilosa* community. DCA axis 1: eigenvalue = 0.43; variance = 8%; Lengths of gradient = 2.48; DCA axis 2: Eigenvalue = 0.28; variance = 6%; Lengths of gradient = 2.33

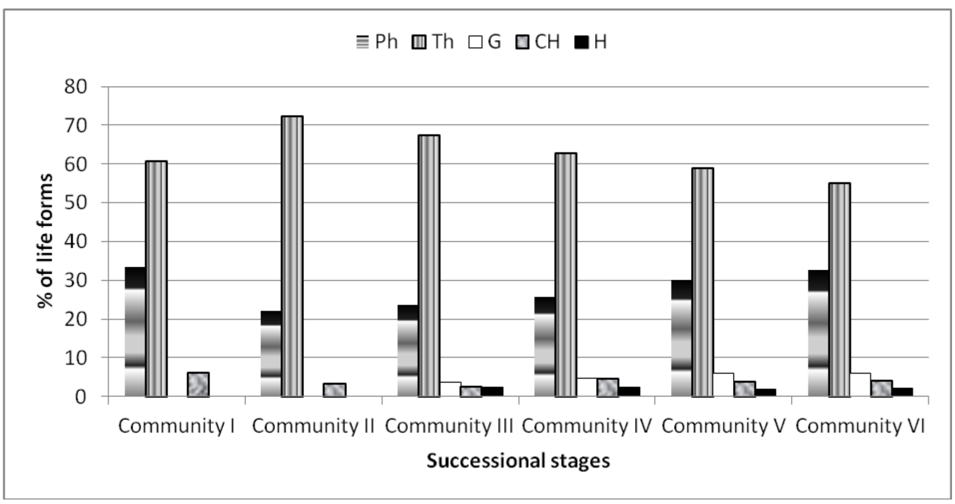

Figure 5. Changes in successional stages raw spctrum of life forms: Ch = Chamaephyte, H = Hemycryptophyte, McPh = Microphanerophyte, MgPh = Megaphanerophyte, NnPh = Nanophanerophyte Th = Therophyte

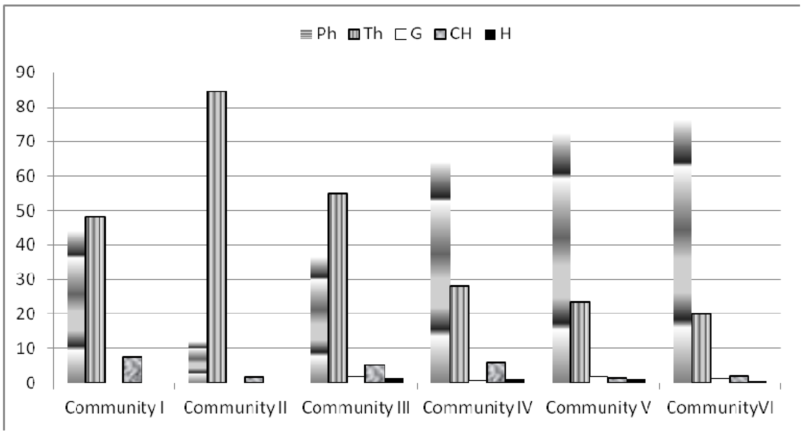

Figure 6. Changes in successional stages weighted spectrum of life forms**:** Ch = Chamaephyte, H = Hemycryptophyte, McPh = Microphanerophyte, MgPh = Megaphanerophyte, NnPh = Nanophanerophyte Th = Therophyte

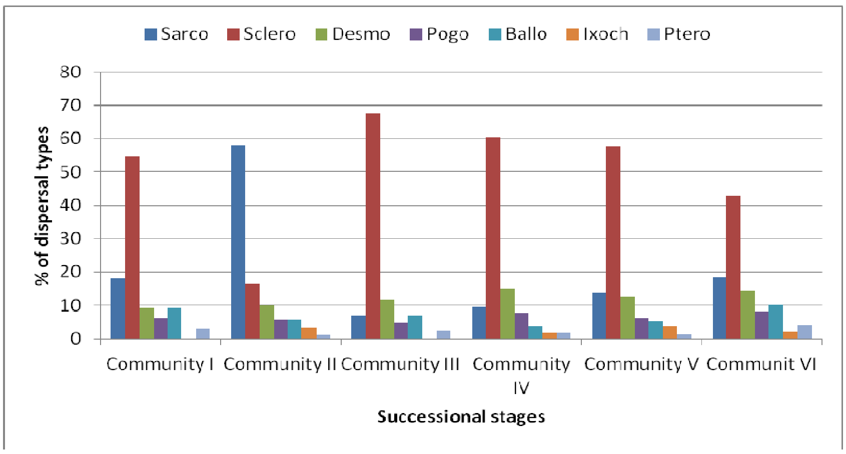

Figure 7. Changes in successional stages raw spectrum of plant species dispersal types: Auxo: auxochore, Ptero: pterochore, Pogo: pogonochore, Desmo: desmochore, Sarco: sarcochore, Sporo: sporochore, Sclero: sclerochore, Ballo: ballochore

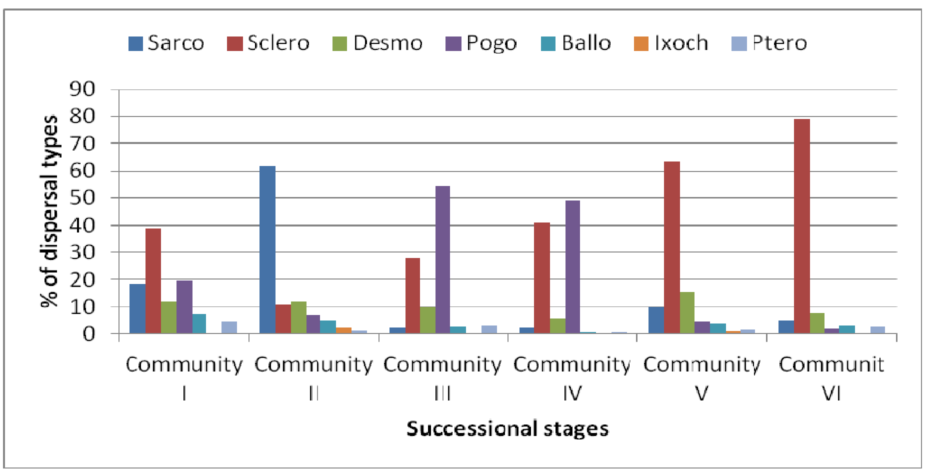

Figure 8. Changes in successional stages weighted spectrum of plant species dispersal types: Auxo: auxochore, Ptero: pterochore, Pogo: pogonochore, Desmo: desmochore, Sarco: sarcochore, Sporo: sporochore, Sclero: sclerochore, Ballo: ballochore

3.4 Changes in Land Conditions

The temporal changes of plants communities, composition, structure and life traits are associated with the changes of sites characteristics (Table 3). Compared to the unrevegtated area (stage I), soil pH, electricity conductivity, soil organic carbon (SOC), the contents of organic matter (OM), available phosphorus (Pa), Calcium (Ca), Magnesium (Mg), Sodium (Na), exchangeable bases (S), cation exchange capacity (CEC) and the S/T ratio (T= total cations) are significantly higher at the revegetated sites ($P < 0.05$) and these parameters increase signifcantly with the restoration ages ($P < 0,05$). The highest values of this parameters are recorded at the late successional stage (stage IV), followed successively by the stages III and stage II. The stage I (unrevegetated site) which has the highest disturbance level, indicates the lowest values of these parameters.

Table 3. Means means±standard error of soil variables for each successional stage (SOC = soil organic carbon, OM = Soil organic matter, P av = available phosphorus, Ca++ = calcium, Mg++ = Magnesium, CEC = Cation exchange capacity, S = total basic cations)

Soil paramaters	PH	SOC (%)	OM (%)	P av (ppm)	Ca++ (méq/100g)	Mg++ (méq/100g)	S	CEC
StageI	3.84±0.07a	0.16±0.14a	0.28±0.25a	5.54±0.23a	2.03±0.45a	1.18±0.29a	3.11±0.41a	5.38±0.25a
Stage II	4.14±0.09b	0.72±0.05b	1.13±0.21b	5.72±0.30b	4.05±0.41b	1.10±0.26a	4.69±0.72b	7.34±0.23b
Stage III	4.70±0.14c	1.51±0.28c	2.600.48c	6.02±0.50c	4.33±0.81b	1.83±0.42b	6.19±0.44c	9.38±1.25c
Stage IV	5.02±0.19d	2.51±0.29d	4.79±0.20d	7.43±0.43d	10.40±0.28c	4.05±0.75c	13.84±0.23d	17.00±0.82d

Means within column with the same letter are not significantly different ($P > 0.05$) based on Tukey–Kramer comparisons.

3.5 Determinants of Successional Changes

Ordination has been repeated with CCA combining the floristic and the environmental variables data sets (Figure 9). The lines length of the CCA diagram indicates the strength of the correlation between plant communities and the environment, the angle between two lines represents their relativity. The first axis of the CCA (Eigenvalue = 0.63 ; variance of species-environment relation = 27,2%) showed strong negative correlations with restoration ages (r = -083), herbaceous heigt (r = -0.74), % of plants cover (r = -0.76), % of litter cover (-0.79), contents of soil organic carbon (SOC, r = -0.72), available phosphorus (Pav, r = - 0.79), calcium (Ca, r = -0.76), Magnesium (Mg, r = - 0.76), total basic cations (S, r = - 0.77) and Cation exchange capacity (CEC, r = - 0.71); and strong positive correlations with % of gravel cruts cover (r = 0.54), % of erosive crust (r = 0.57) and % of barren soil (r = 0.76) (Table 4). The second Axis (Eigenvalue = 0.39 ; variance of species-environment relation = 17%) is correlated with these variables ($r < 0.50$) while the third axis (Eigenvalue = 0.32 ; variance of species-environment relation = 14%) is negatively correlated with % of barren soil (r = - 55); and positively correlated with % of plants cover, contents of soil organic carbon (r = 0.50), soil organic matter (OM, r =0.55). Indeed, the first CCA axis which has the highest values of eingenvalue and variance explains more the distribution of the information. This axis can be interpreted as a gradient of chronological recovering of herbaceous heigt, plants ground cover, litter ground cover, contents of soil organic carbon, available phosphorus, calcium, Magnesium , total of basic cations and Cation exchange capacity; and reducing ground covers of gravel cruts, erosive crusts and barren soil. The Monte Carlo permutation test indicates which of the environmental variables have significant effet on the successional changes of plants communities. Among the tested 16 variables, only the cover of alga (P = 0.7) crusts was found to not have significant effet on the sucessional changes of plants community (Table 4). Moreover restoration age, covers of gravel crusts, erosive crusts, barren soil, plants and litter, soil pH, soil contents of organic carbon, organic matter, available phosphorus, calcium, magnesium, total of basic cations and Cation exchange capacity have significant effets on plants succession ($P < 0.05$). Restoration age, covers of plants and litter, soil pH, soil contents of organic carbon, organic matter, available phosphorus, calcium, magnesium, basic cations and Cation exchange capacity seem to enhance succession of plants communities while covers of gravel crusts, erosive crusts, barren soil restrict succession.

Table 4. Correlations between canonical axis and environmental variables, F-ratios and P-values from Monte Carlo permutation test

Environnemental variables	Axis 1	Axis 2	Axis 3	F-ratio	P-value	Number of Permutation
Ages	-0.83	0.03	0.46	2.63	0.001	999
% of alga crusts	-0.03	0.05	0.02	0.83	0.7	999
% of gravel crusts	0.54	0.44	0.31	1.93	0.001	999
% erosive cruts	0.57	-0.11	-0.2	1.37	0.04	999
Herbacious heigt	-0.74	0.17	0.48	1.5	0.01	999
% of barren soil	0.76	0.04	-0.55	2.43	0.002	999
% of plants cover	-0.76	-0.04	0.54	2.44	0.002	999
% of litter cover	-0.79	0.23	0.4	1.87	0.001	999
pH	-0.44	0.34	0.42	1.48	0.009	999
SOC	-0.72	0.09	0.5	1.43	0.01	999
OM	-0.4	-0.06	0.55	1.31	0.02	999
P av	-0.79	0.26	0.35	2.52	0.002	999
Ca	-0.75	0.14	0.4	2.42	0.002	999
Mg	-0.76	0.17	0.38	2.46	0.002	999
S	-0.77	0.17	0.42	2.09	0.001	999
CEC	-0.71	0.05	0.46	184	0.002	999

(SOC = soil organic carbon, OM = Soil organic matter, P av = available phosphorus, Ca++ = calcium, Mg++ = Magnesium, CEC = Cation exchange capacity, S = total of basic cations).

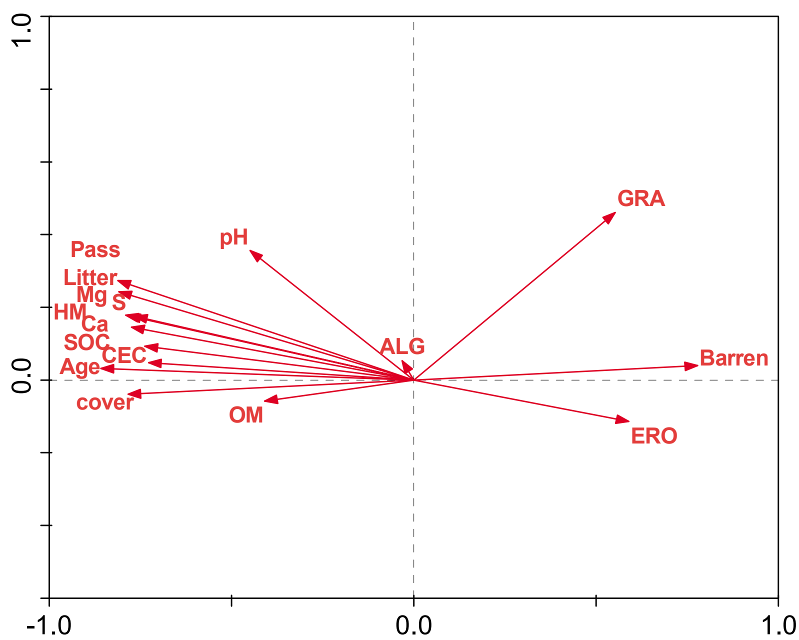

Figure 9. CCA result showing correlation between axis and environmental variables: GRA= % of gravel crusts, ERO = % of erosive soil cover, ALG= % of algal crusts cover, Barren = % of bare soil cover, HM = mean height of herbaceous layer, SOC = soil organic carbon, OM = Soil organic matter, P ass = available phosphorus, Ca = calcium, Mg = Magnesium, CEC = Cation exchange capacity, S = total of basic cations. CCA axis 1: Eigenvalue = 0.63 ; variance of species-environment relation = 27,2%; CCA axis 2: Eigenvalue = 0.39 ; variance of species-environment relation = 17%

4. Discussion

4.1 Mechanism of Succession

The Classification of the vegetation data from the unrevegetated and the revegetated sites of the lateritic plateau with TWINSPAN, provides succession patterns of vegetation, which trajectory is shown by the DCA graph, shifting from unrevegetated to old restored sites. The temporal changes of plant communities was also evident within plants composition, cover, life forms and dispersal types and community structure. Result from the CCA indicates significant relationships between changes in plant communities and changes in sites and soil condition such as covers of physical and erosive crusts, plants, barren soil, soil pH, nutrients content, etc.

The initial extremely stressful stage with compacted soil, without soil legacy, high cover of physical and erosive crusts, barren soil, and low pH and nutrients content prevents seeds germination and seedling survivor. Only some species that have chance to establish on favourable microsites during dispersal of their seeds and stress toleratores could be able to develop in such harmful condition. Favourable microsites are rare in high degraded lands as sahelian degraded plateau, but rocks of the gravel crusts (rocks), algale crusts, local microtopography, wood branches can act as obstacles that would increase soil rugosity, which would trap wind blown soil, nutrients, organic matter and seeds. Accumulation of soil, nutrients and organic matter may create microsites favourable to seed germination and seedlings developpement (Elmarsdottir, 2003). Much of the herbaceous species recorded on the unrevegetated site were occured on those microsites. Although favourable microsites are uncommon and meet by chance by dispersal seeds, the extreme stressful part of the plateau restricts vegetation establishment. Plants recorded on the stressful part may be probably remanent phanerophytes from the undegraded former tiger bush like *Boscia senegalensis* (Pers.) Lam. Ex Poir., *B. angustifolia* A. Rich. and *Maerua crassifolia* Forsk, and herbaceous stress tolerators. Old remanent phanerophytes, annual stress toleratores plants (therophytes) and other plants carried by chance on the rare suitable microsites may be able to develop under such condition. Most of the phanerophytes recorded are sarcochorous, totally fleshy diaspores which dispersal can be ensured by zoochorous. The other phanerophytes are either sclerochorous, pterochorous, ballachorous or pogochorours, but they are less abundant. The therophytes stress toleratores may have developed adaptive traits linked to stress condition: high ecological amplitude, and reproductive capacity, morphological, genetic and plasticity adaptive traits. According to Grime (1979), the traits characteristics of stress tolerates plants are large seeds, long life, slow maximum growth rate and limited response to nutrient lowness. Most of the therophytes are anemochorous seeds dispersed by wind, it can be expanded on large areas. The most abundant and dominant anemochorous are sclerochorous seeds, followed by the desmochorous and the pogonochorous, and the less one are the ballachorous and the pterochorous. As suitable microsites are rare on degraded plateau, the probability to meet them is weak, succession is likely driven by some stress tolerators. This may explain the poorly rate of natural succession on degraded plateau, which can be assimilated to primary succession, consistent with succession on the new volcano substrate (del Moral & Wood, 1993; Fridriksson, 1987; del Moral et al., 2010), glacial moraines (Cooper, 1923 ; Chapin III et al., 1994), sand dunes (Lichter, 2000), mines (Norman et al., 2006) and abandoned fields (Webb et aI., 1986; El-Sheikh, 2003). etc. Infact, abiotic limitations due to rare safe microsites and stressful land condition; and biotic limitation due to schastic event of seeds dispersal on safe microsites seem to be the major factors driving primary succession on degraded plateau. These factors act as ecological filter that restrict plants recovery. Certainly, enhancing chance to trap wind blows seeds by suitable microsites may increase the rate of succession on degraded lands. This can happen by either planting directly in suitable microsites or manipulating the degraded lands to increase the surface of suitable microsites. Thus, land condition seems to be determinant environmental variables affecting succession.

The second stage is associated with direct manipulation (treatment) of the land surface and planting nurses species to increase the rate of succession. They induce rapidly establishment of herbaceous on the restored site showing the highest abundant and dominant of therophytes compared to the untreated area and the old restored sites. In spite of the poorly soil with low organic carbon, organic matter, available phosphorus, calcium, Magnesium, basic cations and Cation exchange capacity, the soil moisture and structure is impoved with the preparation of the land surface by creating half moons and planting nurse plants. They rapidly increase water infiltration, and help to stop runoff, trap wind blows seeds, soil, soil organic matter and nutrient (Soumana et al., 2014). The simple improvement of water holding capacity and limitation of capital resources depletion without adding any nutrients, peaked the plants composition at this stage but the cover steals lower compared to the old restored sites, similar to early secondary succession observed on poorly substrates that present low soil or biological legacy like old fields (Guariguata & Ostertag 2001; Cramer et al., 2008). Low water holding capacity and capital resources depletion such as soil organic matter, nutrients and seeds due to high runoff and soil erosion were known to limit vegetation establishment and vegetation (Tordoff et al., 2000; Bochet &

Garcıa-Fayos, 2004) and the negative effect of low watter holding is accentuated in the Sahel by the high period of the dry season (above nine month per year). At this stage, the dispersal types spectrums is characterized by the abundant and the dominant of zoochorous since the proportion of sarcochorous is higher, similar trend of dispersal mechanism has been observed on abandoned fields, secondary forests (Mosango & Majaliwa, 2008) and falows (Bangirinama, 2010; Faye, 2010) under secondary succession. Although dispersal mechanisms promoting seed arrival from distance sources are more important in primary succession (del Moral & Clampitt, 1985), those promoting burried seeds are more important in colonization of secondary succession sites (Walker & Chapin, 1987). In fact most of the sarcochorous may be buried seeds, unable to grow in stressful condition, the anti-erosive system enhances the humidity of soil that facilitate the growth of burried and arrived seeds that increase the plants composition of the sites that peaked species number. The restoration treatment enhances the environment to facilitate the growth and the developement of plant communities and the exclusion of some plants due to competition for capital resources is weak because of the low vegetation cover. This attest the facilitation effect of the restoration treatment at early stage of restoration, reliable with the facilitation mechanisms of Connell & Slatyer (1977), the inhibition mechanisms are weak due to absence of competition among plants species. Indeed, at early stage of restoration, faciltation mechanisms of restoration treatment may be more important. In the present study, the treatment rapidly facilitates the establishment of the therophytes that may also facilitate the stablishment of later-successional species by enhancing soil surface and adding organic matter to the incipient, which increases soil holding capacity and the availability of nutrient like carbon, nitrogen, etc. (Olson, 1958). The characteristics of therophytes of early stage of succession is well described: short life-spans, fast growth, and produce numerous small easily dispersed seeds. Likely, in poorly soil, high soil water holding capacity seems to be determinant for pioneering plants recovery and soil capital resources availability, similar result was observed by Prach et al., (2014) on restored sites.

Progressively, plant communities change substantially within land condition with increasing restoration age. Land physical crusts and the cover of barren soil were reducing with time, while plants and litter covers, pH, contents of SOC, OM, Ca, Mg, total of basic cations, Cation exchange capacity, available phosphorus were increasing. Analogous observations have been made by Soumana et al., (2014) on restored crusted soil. Time appear to be of one the most important factor affecting changes in plants communities and soil variables (Prach et al., 2014; Soumana et al., 2014). Factors that change with restoration ages may have their intermediate rate at the middle stage. In this study, stage III is considered as middle stage, e.g. likely, it's plants and litter covers, PH, contents of SOC, OM, Ca, Mg, total of basic cations, cation exchange capacity, available phosphorus are lower than in the old restoration stage and greater than the initial restoration and the unrevegetated stages. At stage III, two plants communities have been identified: *Aristida adscensionis* - *Cenchrus prieurii* (Community III) and *Acacia Senegal-Stylosanthes erecta* (IV) communities. We have also identified two plants communities at stage IV (late stage): *Acacia- nilotica- Microchloa indica* community (V) and *Ziziphus mauritiana- Eragrostis pilosa* community (VI). There are similarities of life forms spectrums between communities II and III, and between commuties IV and V. As community III is formed with plots recorded in 3-6 years restorations sites, community V is formed with plots recorded in 6-14 years restoration sites, community III can be considered as transition state between stages II and III, and community V as transition stage between satges III and IV. Similarties of dispersal wheighted spectrums between commuties III and IV and between V and IV that allowed us to classify the six plants communities into four successionnal stages: Stages I and II with one plants community each and stages III and IV with two plants communities each. Anemochorous dispersal types as sclerochorous are known to decrease with succession while zoochorous seeds such as sarcochorous increase (Koubouana et al., 2007; Bangirinama, 2010). But, in the present study, sclerochorous seeds rain still dominant at the old stages. The life forms spectrums are characterized by the timely increasing of the abundance and the dominance of the phanerophytes and the reducing of the therophytes onces. Although, therophytes are respectively abundant at all the stages of succession and dominant at early stages, phanerophytes become dominant at the late stage, and this dominance increases with restoration age, consistent with secondary succession on fallows (Bangirinama, 2010). The substancial increase of litter covers, pH, contents of SOC, OM, Ca, Mg, total of basic cations, Cation exchange capacity, available phosphorus enhance soil structure and nutrient cycling. The CCA attests the significant effet of this soil variables on succession. The effect of the merely preparation of lands with anti-erosive system and plantation have been largely discussed by Soumana et al. (2014). The present study show clearly how this treatment improved soil variables with restoration stages. Surely, mineralization of nitrogen and cycling of available organic mater from litter may play an important role in nutrient availability and soil structure enhancing, these factors have been described by several studies as determinant factors of succession. Inially, the soil has low pH, the availability of SOC, OM, P, Ca, Mg total of basic cations, cation exchange capacity were highly correlated with pH. Thus, acid soil can limit succession. It's largely described that plants community changes with soil variables such as pH, contents of SOC, OM, Ca, Mg, total of basic cations, cation exchange capacity (Wardle et al., 2004). Generally, changes in soil condition may take centuries or even millennia on lands under primary succession such as lava, mines wastes, etc. In the present study, change in land condition has taken very little time due to the restoration treatments. Hence, anti-erosive system and plantation may have great potential to improve rapidly land condition. Reducing plants composition with increasing plants cover has been analyzed by several studies, it has much been linked to competition for capital resources like light and nutrients, consistent with inhibition mechanisms of succession of Connell and Slatyer (1977). Although therophytes number and cover decrease with succession age, the phanerophytes ones increase, thus phanerophytes are tolerated when therophyes are exluded. The tolerance of phanerophytes and the exlusion of therophytes with succession age obeyed successively to the tolerance and inhibition mechanisms of succession of Connell and Slatyer (1977). Timely declines of therophytes may be linked to their inability to compete with late-successional competitive dominants (Prach et al., 1997). Likely, plants succession on restored plateau of western Niger may obey to Connell and Slatyer (1977) mechanisms of succession. Hence, these observations have been done at early stage of succession on restored plateau, the situation could be different at late stage.

4.2 Models of Restoration

Models of restoration ecology were inspired from the models of community assembly advanced in ecology to conceptualize temporal framework of degraded ecosystem recovery. The importance of these conceptual approaches including gradual continuum, thresholds and alternative stable states, to restore dryland systems are widely recognized (Parker, 1997; Suding & Hobbs, 2009; Evans, 2012; James et al., 2013). These models are useful tools to adjust land management and to simply communicate land condition to diverse stakeholders (Knapp et al., 2011; James et al., 2013). According to the DCA graph, the model of restoration of the degraded plateau seems to present one fixed pathway of recovery shifting from the unrevegetated site plant community to the old restoration stage plants communities, between the plant communities of the early and the old stages of restoration, we have the intermediate stage plant communities. But in the intermediate stage (stage III), the pathway seems to diverge in two trajectories then converge in the early stage. In this study, divergence may be more likely to occure at intermediate stage when environmental variables have intermediate rate of factors of succession; and convergence at late stage, when environmental are at their optimum. According to MacDougall et al. 2008, divergence occure mainly in stressful habitats when different species arrive first and where climatic factors are highly variable. Likely, convergence to a single pathway, may occure in mature vegetation when climatic factors dominate, and there is evidence that when dispersal effects are small and competitive effects are strong (Anthelme et al., 2007; Navas & Violle 2009). Indeed early succession under restored plateau can include different pathways: divergence and convergence, analogous with del Moral et al. (2010) on barren surface. Each of the intermediate and the old stages of trestoration is structured by more than one plants communities, consistent to the alternative states model (Knowlton, 1992). Thus, the model of restoration of the degraded plateau may be closer to alternative stable states model. According to Temperton et al. (2004), the model of alternative state reflects reality in nature, its potential in conceptualizing models of rangland restoration and management is widely commented (Hobbs & Norton 1996; Suding & Hobbs, 2009; James et al., 2013). Actually, it’s largely used in forming States and transitions model (STMs) and two-threshold model to achieve either management or restoration goals (Briske et al., 2005; Wilkinson et al., 2005; Spooner et al., 2006; Koch, 2007). Despite the use of this model to guide restoration actions, they provided quantitive framework for predicting effects of management and ecological conditions on restoration outcomes and vegetation state changes (James et al., 2013).

5. Conclusion and Implication for Restoration

To achieve restoration goals, restoration ecologists have developed several tools including models of ecosystems recovery and land prepation techniques. Although these tools have been implemented under different restoration and widespreaded worldwide, still failure subsits. Most of the practitioners suggest to advance conceptual models that allow manipulation of particular ecological processes that initiate autogenic processes directly to self-sustaining ecosystem. In this study, it’s appeared that lack of infiltration due to compaction and physical crusts; depletion of soil nutritents, organic matter and seeds due to erosion, limitation of suitable microsites, stochastic dispersal are the major processes that limit recovery. Merely planting of nurses species in half moons helped to overcome these threshold relating to those processes. After restoration treatment, plant community changes rapidely with restoration age and associated environmental variables. In the early stage of restoration plants community, plants composition peak when cover still lower, then plants cover increase with restoration age while plants composition decreases. As attested by several succession studies, the timely declines of plants composition is associated to inhibion mechanism (competition) and early increases of plants is associated with the facilitation effect of the nurse plants and land preparation. Facilitation effect of early therophyte colonists also increases the number of phaneophytes. Succession on restored plateau represents a complex of timely community change along which plant species are differently affected by changing in environmental condition. The unrevegetated plants community is characterized by potential stress related to lack of infiltration due to compaction and physical crusts, capital resources (soil nutritents, organic matter and seeds) depletion due to erosion, limitation of suitable microsites and stochastic dispersal. The early restored plants community is characterized by poorly soil with high water holding capacity and high species recruitment due to high anemochorous and zoochorous seed rains. But, the late stage is characterized by high plants and litter covers, pH, contents of SOC, OM, Ca, Mg, total of basic cations, Cation exchange capacity, available phosphorus, respectively limitation and increase of therophytes and phanerophytes recruitements. Since plants cover is high at late stage, interaction like inhibition, facilation and tolerance mechanisms, between plants species seems to be high. Although, in the late plants communities, inhibition mechanisms relates to competition for light and nutrients seem to be high, at the middle plants communities facilitation and tolerance mechanisms seem to be higher (c.f. Connell and Slatyer, 1977). Before converging to the late plants community, the restoration pathways can be divergent depending the intensity of local disturbances. Since the middle and the late succession stages can be structured by more than one plant communities, the model of succession on degraded plateau seems to be closer to the alternative stable states model. The model proposed by the present study can be more elaborated by using long term restoration data.

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