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Secondary succession in abandoned fields of dry tropical Northern Cameroon

Donfack, P.[1], Floret, Christian Ch.[2*] & Pontanier, Roger R.[3]

[1]Institut de la recherche agronomique, BP 33, Maroua, Cameroon; [2]ORSTOM BP 1386, Dakar, Senegal and CNRS/CEFE, BP 5051, 34003 Montpellier, France; [3]ORSTOM, BP 434, Tunis el Menzah 4, Tunisia;
*Corresponding author; Fax +221 324387; +33 1 48030829

Abstract. This study evaluates the processes of recolonization of abandoned fields by native vegetation under conditions of intensive human activity (fire, intensive grazing, firewood cutting) in a semi-arid tropical region savanna of northern Cameroon. Secondary plant succession was studied in two series of formerly cultivated fields 1-35 yr after the beginning of the fallow period. Floristic changes and the dynamics of woody plant populations were compared between areas with vertisols (clay texture) and sandy soils, as a function of length of fallows. Vegetation changed continuously during the 35 years following field abandonment. However, a very abrupt break occurred between 6 and 10 yr, due to increasingly intense human pressure during this period. Up to that point, ecological models and mechanisms of succession presented in the literature are more or less confirmed by our results. Usually, secondary succession is blocked at a stage of wooded grassland as a result of human activities.

Keywords: Africa; Fallow; Land use; Plant succession; Savanna; Semi-arid tropical.

Nomenclature: Hutchinson et al. (1954-1972).

Introduction

The purpose of the present study was to evaluate the processes of recolonization of abandoned fields by vegetation under conditions of intensive human activity (fire, intensive grazing, and browsing firewood harvesting) in a semi-arid tropical African savanna region. In particular, we sought to determine whether the classic models of plant succession (Lepart & Escarré 1983) hold under these conditions.

Numerous studies of savanna vegetation dynamics have been carried out (Breman & Cisse 1977; Walker 1981; Grouzis 1988; Le Houérou 1989; Young 1989; Skarpe 1992), but studies of old-field dynamics in dry savanna regions are more rare. In Africa, for example, post-cultivation dynamics have been frequently studied in humid areas where itinerant slash and burn agriculture predominates (Guillaumet 1978; de Namur 1978; Alexandre et al. 1978; Kahn 1982; Mitja 1990), but vegetation dynamics in fallow fields in drier areas, where human pressure is generally stronger and more continuous, have not been thoroughly studied (but see Devineau 1986; Yossi & Floret 1991; Donfack 1993b; Floret & Serpantié 1993; Floret et al. 1994).

The study addresses the secondary succession or 'regeneration succession' (van der Maarel 1988) following field abandonment in the dry tropical African savanna region. In many parts of dry tropical Africa, much of the land cleared for agriculture is abandoned after a few years, due to invasion of aggressive weeds or a drastic decline in soil fertility. While some fields remain permanently abandoned, the majority are cultivated again as soon as judged possible. Thus the region forms a patchwork of cultivated fields and wooded savanna or wooded grassland (*sensu* White 1983) where the woody plants cover between 10 and 50 % of the surface. Pseudo-climatic dry forest with woody cover of > 80 % is found in a few more or less protected sites which are never cultivated.

Material and Methods

The study was carried out in northern Cameroon, between 10° and 12° N, in a region with a Sudano-Sahelian climate, i.e. 700 - 900 mm mean annual precipitation falling between June and October. Maximum temperatures exceed 37 °C between March and May and minimum temperatures are 16 - 17 °C between December and February. The abandoned fields included in the study were all situated on plateaus or plains (ca. 700 m altitude) underlain by gneiss (Seiny Boukar 1990; Donfack 1993a,b) between the Benoué valley and the Chad basin. Two major soil categories can be distinguished in the region:

(1) coarse-grained fersiallitic or sandy ferruginous soils (Duchaufour 1977) on hard pan with primarily kaolinic clays;

(2) heavy vertisols (Duchaufour 1977) where montmorillonitic clays are abundant.

We analyzed the variation in floristic composition

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and plant community structure in plots of differing ages following the abandonment of agriculture. 'Phyto-ecological' (phytosociological) relevés were carried out following the protocol of Gounot (1969) and exhaustive inventories of all woody plants were made at each site.

The age of the fallows was determined from interviews with local farmers combined with ring counts of the cross sections of the woody species that coppice after cutting or burning. Because there is a short, clearly defined growing season and a long dry season, annual growth rings can be distinguished in most woody species in the study area (Mariaux 1979; Donfack 1993b).

Relevés

Site selection was based on two criteria: age of the fallow, i.e. the number of years since the abandonment of agriculture, and soil type. At each site, we noted details of the recent history as well as existing vegetation and ecological characteristics. Minimum plot size was 64 m^2 for the herbaceous plants and 2000 m^2 for the woody plants; the smaller plots were nested inside the larger ones. The relevés consisted of a complete species list for each plot.

170 relevés were made during the period 1989-1990 (Table 1). Physical site characteristics and floristic data obtained were used to create a computerized data base using BASEFLO (Le Bourgeois & Grard 1988). At all sites, the distribution of each species in the different classes of each ecological variable was quantified. The use of information theory (Abramson 1963) in general, and the mutual information technique in particular, has often been used in phyto-ecological studies, notably by Godron (1968), Gounot (1969), Guillerm (1971), Daget et al. (1972), Moris & Guillerm (1974) and Bottliková et al. (1976). The test of Gauthier et al. (1977) was used to quantify the positive or negative correlation of a given species with a given ecological variable (e.g. in the current study, fallow field age). The analysis allows the characterization of the autecology of the species found and their grouping into different classes of the variables (Fig. 1). Groups of 'indicator species' were established on the basis of their presence/absence. It should be stressed that the method does not seek to describe vegetation stages, but to determine which species are best correlated with a particular stage. Thus, dominant species or those found in most relevés do not appear in the results. Rare species also provide little information and are not considered in the results. A Factorial Analysis of Correspondence was also used to link fallow age with the dominant species present.

Woody plant dynamics

Spatial and temporal dynamics of the woody stratum were studied in plots of 900 m^2 on both ferruginous soils and vertisols. For each soil type, three stages of field abandonment were considered: the initial stage (1 yr), the intermediate stage (6 - 12 yr), and the most advanced stage observed for each soil type - 15 yr on vertisols and 25 yr on ferruginous soils. Three replicate plots were sampled per age category and soil type.

In each plot, the age and height of the main stems of all woody plants were determined, as well as the number of coppice shoots. The smallest shoots were systematically cut 5 - 10 cm from ground level in order to count annual growth rings of the main stem. For larger plants (stem diameter > 10 cm), we extracted stem cores with the aid of a Presler core sampler. We also noted the method of establishment for each individual: seedling or stump regrowth.

Results

Floristic composition and age of fallows

In the study area we recorded 439 plant species. Of these, 44 were selected as providing the most information on fallow field age. Four groups of indicator species can be distinguished on the basis of probability of their occurrence in fallows of differing ages (Fig. 1).

Group 1 includes primarily invasive pioneer species, all of which are annuals with shallow root systems. Some of these, such as *Leucas martinisensis*, are also found in older fallows under the shade of woody plants. Herbaceous species normally characteristic of uncultivated savannas or older fallows, e.g. the grasses *Eragrostis tremula* and *Pennisetum* spp., also occur here, but only occasionallly in sites where adjacent undisturbed

Table 1. Distribution of sampling sites on the basis of soil type and fallow field age.

Fallow type / Code	Culture	Fallow AG_0	Fallow 1 - 2 yr AG_1	Fallow 3 - 4 yr AG_3	Fallow 5 - 9 yr AG_5	Fallow 10 - 22 yr AG_{10}	Total > 22 yr AG_{23}
Ferruginous & fersiallitic soils (light texture)	15	19	20	17	16	12	99
Vertisols (heavy texture)	12	14	08	12	14	11	71
Total	27	33	28	29	30	23	170

Species	AG_0	AG_1	AG_3	AG_5	AG_{10}	AG_{23}	
Corchorus tridens	+	0	0	0	-	-	
Digitaria ciliaris	+++	0	0	0	0	0	
Eragrostis ciliaris	+	0	-	0	0		Group 1
Leucas martinicensis	+++	0	-	0	0	-	
Acalypha ciliata	+++	0	0	0	-	--	
Brachiaria lata	+	0	0	0	0	--	
Commelina benghalensis	++						
Eriochloa nubica	-	+	+	0	0	-	
Alysicarpus rugosus	0	+	0	0	0	---	
Cassia obtusifolia	0	++	0	0	0	-	Group 2
Andropogon pinguipes	---	+	0	0	0	-	
Caperonia senegalensis		+++			0		
Calotropis procera	0	+++	0	0	-	0	
Launaea chevalieri		++	0	0	-		
Merremia emarginata	0	+	0	0	0		
Annona senegalensis	-	-	+	+	0	0	
Stylochiton lancifolius	--	0	+	+	0	0	
Chloris pilosa	-	0	+	0	+	-	
Acacia senegal	--	0	+	0	0	+	
Aspilia helianthoides	0	0	+	0			
Mukia madaraspatana	0	0	++	0	0	0	Group 3
Spermacoce radiata	0	0	+	0	0	-	
Lepidagathis heudelotiana	-	0	++	0	-	0	
Tripogon minimus			++				
Dipcadi viride			+				
Eragrostis tremula	0	0	0	++	0		
Cassia singueana	--	-	0	++	0	0	
Piliostigma reticulatum	---	0	0	++	0	0	
Sporobolus festivus	---	--	0	0	++	+	
Acacia ataxacantha	-	-	-	0	+	+++	
Balanites aegyptiaca	--	-		0	++	+++	
Feretia apodanthera	-	-	0	0	+	+	
Andropogon pseudapricus	--	0	0	0	+	0	
Anogeissus leiocarpus	-	0	0	0	++	0	
Cissus cornifolia	--	-	0	0	+++	0	
Pandiaka heudelotii	0	--	0	0	++	0	Group 4
Loudetia togoensis	--	0	0	0	0	+	
Celosia argentea						+++	
Cissus quadrangularis						++	
Combretum glutinosum	---	-	0	0	0	+	
Lannea humilis	0	-	0	0	0	++	
Panicum anabaptistum						+	
Sterculia setigera	0	-	0	0	0	++	
Tamarindus indica	0	-	0	0	0	++	

+ = Presence at 95% confidence level
++ = Presence at 99% confidence level
+++ = Presence at 99.9% confidence level
- = Absence at 95% confidence level
-- = Absence at 99% confidence level
--- = Absence at 99.9% confidence level
0 = Species occurs independently of age class

The absence of a sign indicates that the species was not sampled sufficiently for the calculation of its probability of presence.

Fig. 1. Ecological profile of species as function of fallow field age (based on 170 relevés, 1988-1990). For fallow type, see Table 1.

savannas serve as seed source.

Group 2 contains species that are abundant in one or two-year old fallows. These are primarily annual species, with the exception of *Calotropis procera*, a widespread short-lived tree species (*Asclepiadaceae*) whose germination appears to be restricted to abandoned fields and other disturbed sites. Although few in number, grasses dominate in terms of cover and overall abundance. One of the most important grasses is *Andropogon pinguipes*.

Group 3 consists of species usually found in 3 - 9 yr old fallows. The most common are *Lepidagathis heudelotiana* and *Tripogon minimus*. Here, woody species become progressively more important, including *Annona senegalensis*, *Acacia senegal*, *Cassia singueana* and *Piliostigma reticulatum*. The last species is usually seen after the 4th year of field abandonment. Several grasses and other herbaceous perennials also appear at this stage, e.g. *Stylochiton lancifolius* and *Dipcadi viride*. These species all have a deeper root system than the herbaceous species of groups 1 and 2.

Group 4 includes indicator species for fallow fields more than 10 yr old. The most common species are *Acacia ataxacantha*, *Balanites aegyptiaca*, *Cissus cornifolia* and *Combretum glutinosum* in the woody strata and *Sporobolus festivus* and *Loudetia togoensis* among herbaceous plants. Woody species are numerous in this group and there are no perennial grasses other than *Sporobolus festivus*.

Changes in dominant species during succession

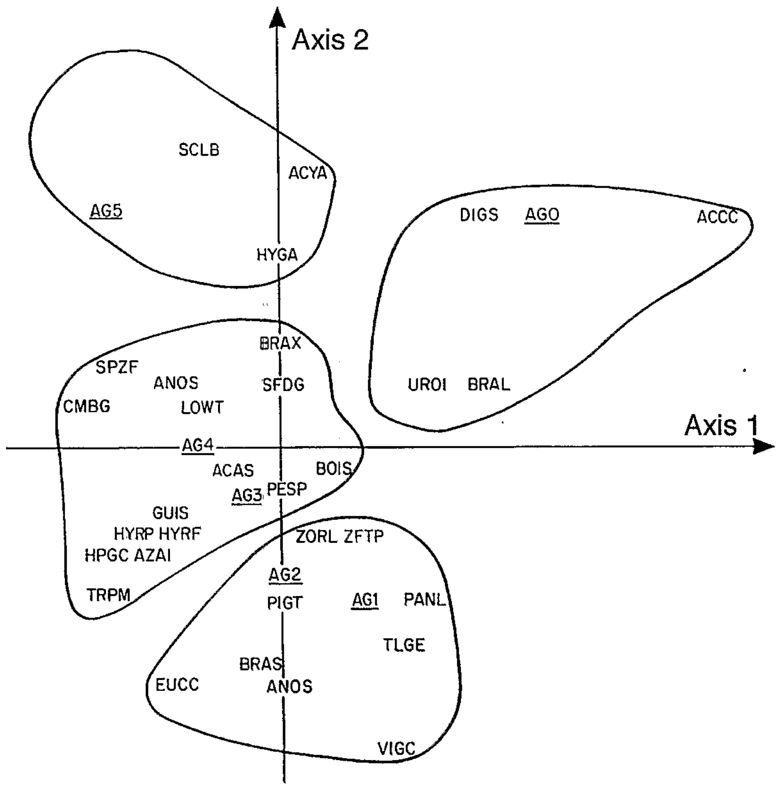
The diagram of the Factorial Analysis of Correspondence shows the distribution in two dimensional space of the age classes on the one hand and the dominant plant species (> 50% cover) found in at least six relevés on the other (Fig. 2).

Apart from fields in cultivation (AG_0), that forms a distinct environment, the other age classes are evenly distributed along axis 2, from bottom to top. For all age classes, there is a general pattern of distribution from young stages on the left to the older on the right. The dominant plant species in these stages follow this distribution without necessarily being grouped by stage. Thus four main groups can be distinguished:

1. The dominant crop weeds, including *Digitaria ciliaris*, *Acacypha ciliata*, *Urochloa trichopus* and *Brachiaria lata*. This group of species is somewhat loose, probably due to differences related to soil type and other important environmental variables.

2. This group includes AG_1 and AG_3; it appears 1 - 4 yr after abandonment and is quite distinct from group 1. Apart from *Piliostigma thonningii*, which is apparently protected by peasants during cultivation, there are no woody species which dominate in the first four years of fallow. However, the dominant herbaceous species are abundant (depending on, *i.a.*, soil type, crop history, climatic characteristics of the year); *Setaria pumila* on vertisols and *Zornia glochidiata* on sandy soils etc.

3. Group 3 appears in stages AG_5 and AG_{10}, 5 to 22 yr after abandonment. It includes species which form the transition from herbaceous vegetation in the early years to woody vegetation on the older fallows. The species dominating in the widely distributed stages are found here, woody species such as *Guiera senegalensis*,



ACAA = *Acacia ataxacantha*
ACAS = *A. seyal*
ACCC = *Acalypha ciliata*
ACYA = *Achyranthes aspera*
ANOG = *Andropogon gayanus*
ANOS = *Anogeissus leiocarpus*
AZAI = *Azadirachta indica*
BOIS = *Spermacoce ruelliae*
BRAL = *Brachiaria lata*
BRAS = *B. stigmatisata*
BRAX = *B. xantholeuca*
CHRP = *Chloris pilosa*
CMBG = *Combretum glutinosum*
EUCC = *Euclasta condylotriche*
DIGS = *Digitaria ciliaris*
GUIS = *Guiera senegalensis*
HPGC = *Heteropogon contortus*
HYGA = *Hygrophila auriculata*
HYRF = *Andropogon fastigiatus*
HYRP = *A. pseudapricus*
LOWT = *Loudetia togoensis*
PANL = *Panicum laetum*
PESP = *Pennisetum pedicellatum*
PIGT = *Piliostigma thonningii*
SCLB = *Sclerocarya birrea*
SFDG = *Schoenefeldia gracilis*
SFTP = *Setaria pumila*
SPZF = *Sporobolus festivus*
SZYE = *Schizachyrium exile*
TLGE = *Thelepogon elegans*
TRPM = *Tripogon minimum*
UROI = *Urochloa trichopus*
VIGC = *Vigna comosa*
ZORL = *Zornia glochidiata*

Fig. 2. Factorial Analysis of Correspondences, axes 1 and 2. Both the four species groups with their dominant species, and the fallow types are indicated. For fallow types, see Table 1.

Anogeissus leiocarpus on sandy soils and *Acacia seyal* on clay soils as well as herbs such as *Loudetia togoensis*, *Sporobolus festivus*, *Heteropogon contortus* and *Andropogon fastigiatus*.

4. Group 4 (AG_{23}) has the trees *Sclerocarya birrea* and *Acacia ataxacantha* as dominant species.

Dynamics of woody species

The present study showed that the frequency of young woody plants is high, irrespective of fallow age (Fig. 3; Tables 2 and 3). Conversely, large mature trees are rare. This conforms the observations of Poupon

Table 2. Age structure of woody plants after a fallow period of 10 years (vertisol). Figures for each species correspond to number of individuals occurring in 900 m² plots.

Species	Years												
	0	1	2	3	4	5	6	7	8	9	10	11	12
Combretum sp.		1											
Phyllanthus sp.		1											
Acacia senegal			1										
A. gerrardii			1										
A. ataxacantha			2										
Lannea humilis		3	1										
Piliostigma reticulatum		4	1	1									
Gardenia ternifolia		7											
Combretum fragans		6											
Cassia singuana	1	5	2	1									
Ziziphus mauritiana	1	2	5	3									
Entada africana		27	2										
Combretum aculeatum	1	17	10	3									
Dichrostachys cinerea		17	9	3	7								
Acacia seyal	17	19	38	48	17	17	13	1	7	4	1		1

Table 3. Age structure of woody plants after a fallow period of 25 years (ferruginous soil). Figures for each species correspond to number of individuals occurring in 900 m² plots.

Species	Years																									
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Acacia senegal		20	8	2	2		1		1																	
Anogeissus leïocarpus		15	6	2	4	4	2			1			1								2			1		2
Combretum aculeatum		2	6	1																						
C. fragans		6						1																		
C. glutinosum		4	1		1	1	1				1															
C. molle			1		1																					
Commiphora africana		3							1																	
C. pedunculata		19																								
Diospyros mespiliformis		1	2	1																						
Entada africana		1	1													1										
Guiera senegalensis		3	3	2																						
Hoslundia opposita	1	47	31																							
Mitragyna inermis		54	18	1	5		1																			
Pentatropis sp.		3	3																							3
Sclerocarya birrea									1			1	1			1					2					
Securinega virosa			6	2																						
Steganotaenia araliacea		3																								
Stereospermum kunthianum		4																								
Ziziphus mucronata			10	5	2																					

Note : 13 additional species, represented by only one individual each, were excluded.

(1980) in a Sahelian savanna of northern Senegal.

Although age structure was studied for all woody species in each plot, We present data only from two plot types: Plot A on a vertisol, Plot B on a ferruginous soil, in order to illustrate the general dynamics of the woody species (Tables 2 and 3). On the vertisol (Table 2), all the pioneer species (*Piliostigma reticulatum*, *Dichrostachys cinerea* and *Combretum aculeatum*) survive after 12 years of field abandonment, but only as young plants. Only *Acacia seyal* has mature individuals, some of which date from the beginning of the agricultural period, probably due to the resistance of *A. seyal* to both fire and browsing. One individual each of *Gardenia ternifolia* and *Ziziphus mauritiana* were also large enough to survive, despite repeated fires and uncontrolled browsing. The great majority of individuals of most woody species are young seedling plants (< 3 yr old). The greatest difficulty faced by woody plants in this environment is not germination or regeneration, but rather developing to adult stages. Human pressures (woodcutting, fire, etc.) tend to block all but the oldest woody specimens at a given site from attaining their full potential size. This trend was observed in all the plots studied. On a ferruginous soil site, fallow for the last 25 years (Table 3), there was also a strong concentration of individuals of all species in the 1-3 yr age class. Individuals older than 6 years were very rare and dispersed. The largest trees were those that were preferred for cutting firewood. There were a few older full-sized specimens of soft-wooded trees (e.g. *Sclerocarya birrea*) that are not useful for firewood, or else are multipurpose tree species such as *Anogeissus leiocarpus*, which are carefully protected by most farmers. Trees most favoured for firewood (e.g. *Combretum glutinosum* and *Ziziphus mauritiana*) are generally not kept beyond the age of 6-

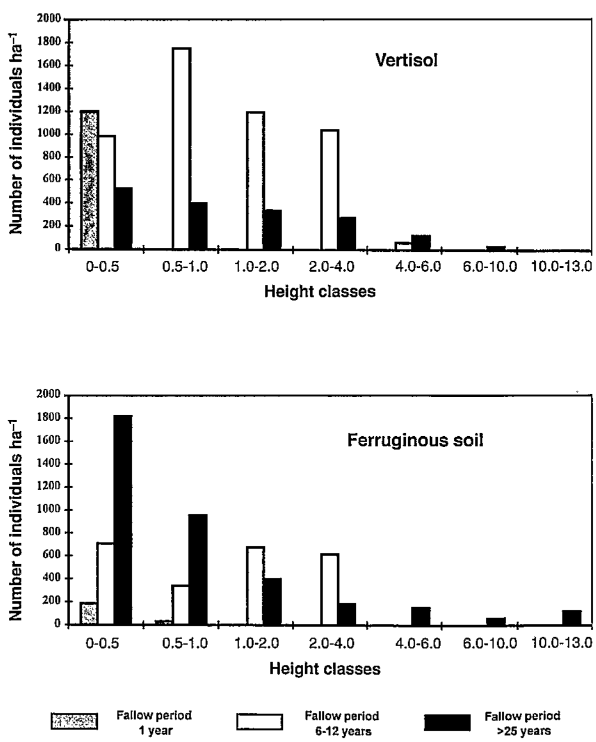


Fig. 3. Height classes of woody species on ferruginous and vertisol soil sites, after a fallow period of 1, 6-12 and >25 yr.

10 years. In sharp contrast to the vertisol sites, with only 15 species (Table 2), in the ferruginous soil sites new woody species appear throughout the fallow period: 32 woody species were present in this 25-yr old fallow (Table 3). This agrees with the general observation of Frost et al. (1986) that floristic diversity is always higher in savannas on sandy soils, doubtless due to more abundant potential microsites characterized by different soil moisture conditions, nutrient contents and the depth of root occupancy.

Each soil type is characterized by a differential group of woody plant species. The self-reconstituting savanna on vertisols does not resemble that of ferruginous soils. The former consists primarily of spiny legume species while the latter is dominated by *Combretaceae* (Tables 2 and 3). Spiny legume species are considered as Sahelian elements, while *Combretaceae* belong to the wetter Soudanien flora (Letouzey 1968). Despite the age difference between these two plots, their tree age class structures were similar, with a preponderance of young individuals in both cases. This trend holds true regardless of the age of the fallows.

The vegetative mode of regeneration clearly dominates compared to the sexual. There are about four times as many coppicing individuals as seedlings in all the plots (Table 4). There is virtually no seedling germination at the beginning of the fallow period and coppicing represents the primary mode of woody plant regeneration in these early stages of savanna revegetation. Although increasing numbers of seedlings do germinate, heavy grazing pressure combined with frequent intentional fires prevents them from growing. They are also cut or burnt back and thus forced to regrow from root crowns at regular intervals.

Discussion

Influence of human disturbance

Even if clearing for cultivation is cyclic or intermittent, it can be considered as disturbance in the sense of Grime (1979) since it implies an almost complete destruction of the existing vegetation. The dynamics and structure of the vegetation arising through regeneration succession depend on the availability of various potential sources of colonization (Noble & Slatyer 1980) and on environmental constraints. Post-agricultural succession is also strongly modified by site history, i.e. by the type, frequency and intensity of stress or disturbance imposed by people both during the agricultural phase and during the period, following abandonment of the field.

Table 4. Mode of establishment of woody species.

Plots	Germination (%)	Stump sprouts (%)	Unknown (%)
Fallow 20 years (Vertisol)	15	80	5
Fallow 25 years (Ferruginous soil)	19	79	2

Perturbations during the agricultural phase

Reconstitution of vegetation, especially in the woody stratum, is heavily influenced by the methods used originally to clear the site, especially the depth at which the field was ploughed. Additionally, the length of the cropping-fallows cycle practised prior to abandonment has a major effect (Mitja 1990). In a shifting system, such as is practised in this region, the majority of cleared fields are cultivated immediately after burning and clearing, i.e. without systematic removal of tree stumps. As a result, when cropping is interrupted after a relatively short time (e.g. 1-5 yr in the area under study), the reproductive potential of the highly diverse, seed bank and of coppicing woody species is high (Mitja op. cit.; Alexandre 1989).

In contrast, Yossi & Dembele (1993) in Mali, and Mitja & Puig (1993) in Ivory Coast noted that when clearing is undertaken with heavy equipment, and deep ploughing removes all woody stumps, the return of woody species is much slower. The reproductive vigour of coppicing species is also finally exhausted in fields cleared without heavy equipment after 15 years of cultivation. In such cases, succession is blocked at the grassland (*sensu* White 1983) or herbaceous savanna stage for many years.

Post-cultural perturbations

Perturbations imposed following field abandonment are more or less regular (intentional fires, grazing and browsing, firewood collection). In the first few years after field abandonment, there is not enough woody material to attract firewood cutters, nor enough mature trees yielding edible fruits to attract people, birds or other animals. This absence of exploitable resources during early succession explains, at least in part, the rapidity of biological reconstitution during the first stages of secondary succession, accompanied by major changes in floristic composition and vegetation structure. Thereafter, when the plant cover becomes greater and woody species attain a usable size, the secondary savanna is again subjected to numerous anthropic pressures. Firewood harvesting becomes increasingly frequent and after woody individuals attain 6-10 yr of age it remains highly selective, gradually leading to scarcity of the most used species, e.g. *Acacia polyacantha*, *A. seyal*, *Albizia chevalieri*, *Anogeissus leiocarpus*.

Grazing and browsing pressure also plays an important role in the dynamics of secondary succession. The principal woody species found in abandoned fields of less than ten years age are *Piliostigma reticulatum*, *P. thonningii*, *Cassia singueana*, *Annona senegalensis*, *Bauhinia rufescens*, *Combretum aculeatum*, *C. glutinosum*, *Dichrostachys cinerea*, *Acacia seyal*, and *Ziziphus mauritiana*, independent of soil type. The majority of these are valuable forage and browse species, constituting an important part of the diet of livestock, especially during the dry season (Le Houérou 1989). Animals thus contribute to the maintenance of a relatively open, low-growing formation, until the trees grow out of their reach. As a result of overgrazing and periodic ploughing, perennial grasses such as *Andropogon* and *Hyparrhenia* spp. are not able to establish in competition with herbaceous annuals in abandoned fields (César & Coulibaly 1990). Woody savanna species in northern semi-arid Cameroon are characterized by considerable regenerative capacity but suffer high mortality rates beyond a certain age and stage of development, due to continually being cut back by firewood cutters, browsed by animals or burnt by bush fires. Only a few isolated individuals escape and eventually overtop a shrub-savanna composed of young individuals forced continually to regrow from the ground level.

The post-cultural secondary succession

Walker (1981) questioned whether succession is a valid concept in savanna zones. In savannas with little or no human disturbance, succession appears to be directional and predictable. Bush fires occur almost every year and can thus be considered to be a regular constraint rather than a perturbation. Given the relatively effective rainfall in the Sudano-Sahelian zone, infrequent droughts do not seem to have much impact on the direction of plant succession.

In early stages after field abandonment, succession does appear to be clear-cut and easily interpreted. In our study area, species that appeared in the early stages or else were already present as weeds in the field before abondonment, are progressively eliminated in the course of secondary succession. They are gradually replaced by others that are better adapted to the new conditions. Herbaceous savanna elements (*Andropogon pinguipes*, *Pennisetum pedicellatum*, etc.) gradually replace the adventitious species of the first fallow stages, and thereafter coexist with the woody species of the latter stages. Most woody species characteristic of the young stages (e.g. *Piliostigma reticulatum*, *Annona senegalensis*, and *Calotropis procera*) survive, as isolated individuals, in later stages as well. Similarly, many species that could dominate the late, 'pseudo-climatic' stages, such as *Acacia ataxacantha* and *Tamarindus indica* (Letouzey 1968), are already present in recently abandoned fields. These observations conform to the 'initial floristic composition' model of Egler (1954) and also the 'tolerance' model of Connell & Slatyer (1977). Post-cultivation reconstitution in dry tropical zones fits the latter model well, since savanna species gradually become established in the abandoned fields without completely displacing the pioneer species that arrived earlier (Mitja & Puig 1993).

The short-term changes that occur during post-cultivation secondary succession in our study area are most dramatic during the early phases. Species remaining from the cultural phase disappear rather rapidly. At all fallow stages over 80 % of herbaceous plant cover consists of annuals, no doubt as a result of strong anthropic pressure. Herbaceous perennials only increase when there is a reduction of pressure on the site.

Vegetation structure under the conditions we have described are the result of human perturbations imposed prior to and after field abandonment. The regulatory factors (Walker 1985) of ecosystem structure and floristic composition are chiefly external in the case of these post-cultivation savannas. Competition for water (and nutrients) between the tree and herb strata and influence of grazing have been discussed as determinants of structure and dynamics of savannas by Walker (1981, 1985), Walker & Noy-Meir (1982), and Knoop & Walker (1985). In Cameroon, Seghieri (1990) has studied this problem on vertisols. Here internal processes, such as competition for water or feedback regulation seems less important than intense human pressure on the vegetation in determining the meta-stable equilibrium observed in savannas 6 yr after abandonment of cultivation. In this Sudano-Sahelian zone at least, high grazing pressure does not appear to increase woody plant cover at the expense of the understorey, as has been described for other regions in Africa (Knoop & Walker 1985; Stuart-Hill & Tainton 1989; Skarpe 1990).

Conclusions

The first years after field abandonment are the most critical as to change in botanical composition of these wooded grasslands or secondary savannas. In contrast, after a period of 6 - 10 yr, an artificial brake is imposed on the succession by local people through the imposition of heavy grazing and selective removal of woody biomass for fuelwood. Some species can be considered indicators of fallow field age, but whatever floristic changes may occur after 6 - 10 yr, they have little effect on the structure of these secondary savannas.

From this it is clear that the successional models for relatively undisturbed vegetation types cannot fully describe or predict post-cultivation succession in the Sudano-Sahelian savanna zone. In this case, prolonged human pressure leaves little room for rare or random events that might modify successional trajectories in models such as that of Westoby (1980). Perturbations such as periodic ploughing, fire, grazing and wood cutting become regular constraints on the system. Man intervenes following the relatively short period when 'natural' succession occurs in order to block the secondary savanna at a meta-stable equilibrium of short-term benefit to people. However, this equilibrium can be lost in the long term through excessive exploitation of woody and herbaceous biomass, or through progressive reduction of the fallow periods (Seiny Boukar et al. 1992; Aronson et al. 1993). The vegetation type that survives this process of succession by degradation is a result of the interaction of the biological characteristics of the principal species with the regular perturbation of land clearing. Extrapolating from the results of this study, the consequences for the vegetation of current trends to shortened fallow periods can be summarized as follows:

1. After the commencement of cultivation, adventive weeds return quickly and massively, since the fallows were not long enough for them to be eliminated through competition (de Rouw 1993).

2. Herbaceous perennials do not have sufficient time to re-establish.

3. Woody species arising primarily from seedlings become increasingly rare.

4. The woody stratum is reduced to species resistant to shallow ploughing by virtue of their root suckering ability (*Dichrostachys cinerea*, *Lannea humilis* and *Combretum aculeatum*) or coppicing capacity (*Piliostigma reticulatum*, *Guiera senegalensis*, *Acacia* spp. etc.). However, even these species can be weakened and eventually eliminated if the cultural phase is prolonged.

The long-term trends of these post-cultivation dynamics lead to savannas with a purely annual herbaceous layer, dominated by scarce woody coppicing species, as can be already seen in the vicinity of many villages or towns in semi-arid Africa. Plant diversity decreases considerably, but the species that persist are well adapted to the regular disturbance of land clearance, which thus tends to become a normal constraint to the system. Competitive exclusion of species does not have time to operate. The vegetation is therefore of low diversity but highly resilient. Among the six connections between disturbance and stability proposed by van der Maarel (1993), the choice could then be disturbance for stability, but at a very low level of productivity.

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