

Secondary succession in abandoned fields of dry tropical Northern Cameroon

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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

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 & Pontanier 1993; Floret & Pontanier 1994).

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 m² for the herbaceous plants and 2000 m² 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

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 m² 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.

| Species | AG ₀ | AG ₁ | AG ₃ | AG ₅ | AG ₁₀ | AG ₂₃ | |
|-------------------------------|-----------------|-----------------|-----------------|-----------------|------------------|------------------|------------|
| <i>Corchorus tridens</i> | + | 0 | 0 | 0 | - | - | Group 1 |
| <i>Digitaria ciliaris</i> | +++ | 0 | 0 | 0 | 0 | 0 | |
| <i>Eragrostis ciliaris</i> | + | 0 | - | 0 | 0 | | |
| <i>Leucas martinicensis</i> | +++ | 0 | - | 0 | 0 | - | |
| <i>Acalypha ciliata</i> | +++ | 0 | 0 | 0 | - | -- | |
| <i>Brachiaria lata</i> | + | 0 | 0 | 0 | 0 | -- | |
| <i>Commelina benghalensis</i> | ++ | | | | | | |
| <i>Eriochloa nubica</i> | - | + | + | 0 | 0 | - | Group 2 |
| <i>Alysicarpus rugosus</i> | 0 | + | 0 | 0 | 0 | --- | |
| <i>Cassia obtusifolia</i> | 0 | ++ | 0 | 0 | 0 | - | |
| <i>Andropogon pinguipes</i> | --- | + | 0 | 0 | 0 | - | |
| <i>Capeneria senegalensis</i> | | +++ | | 0 | | | |

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.

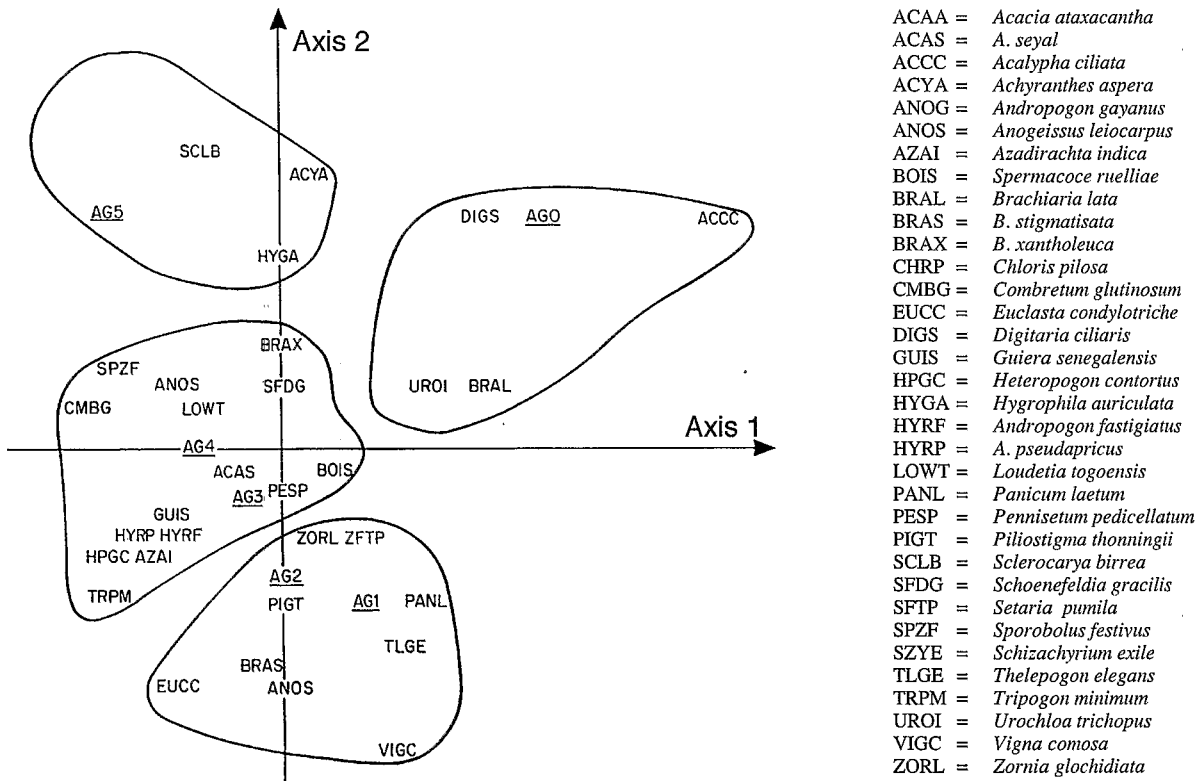


Fig. 2. Factorial Analysis of Correspondences, axes 1 and 2. Both the four species groups with their dominant species, and the fallow types are indicated. For fallow types, see Table 1.

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 (AG₂₃) 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 |
| <i>Combretum</i> sp. | | 1 | | | | | | | | | | | |
| <i>Phyllanthus</i> sp. | | 1 | | | | | | | | | | | |
| <i>Acacia senegal</i> | | | 1 | | | | | | | | | | |
| <i>A. gerrardii</i> | | | 1 | | | | | | | | | | |
| <i>A. ataxacantha</i> | | | 2 | | | | | | | | | | |
| <i>Lannea humilis</i> | | 3 | 1 | | | | | | | | | | |
| <i>Piliostigma reticulatum</i> | | 4 | 1 | 1 | | | | | | | | | |
| <i>Gardenia ternifolia</i> | | 7 | | | | | | | | | | | |
| <i>Combretum fragans</i> | | 6 | | | | | | | | | | | |
| <i>Cassia singuana</i> | 1 | 5 | 2 | 1 | | | | | | | | | |
| <i>Ziziphus mauritiana</i> | 1 | 2 | 5 | 3 | | | | | | | | | |
| <i>Entada africana</i> | | 27 | 2 | | | | | | | | | | |
| <i>Combretum aculeatum</i> | 1 | 17 | 10 | 3 | | | | | | | | | |
| <i>Dichrostachys cinerea</i> | | 17 | 9 | 3 | 7 | | | | | | | | |
| <i>Acacia seyal</i> | 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 |
| <i>Acacia senegal</i> | | 20 | 8 | 2 | 2 | | 1 | | 1 | | | | | | | | | | | | | | | | | |
| <i>Anogeissus leiocarpus</i> | | 15 | 6 | 2 | 4 | 4 | 2 | | | 1 | | | 1 | | | | | | | | 2 | | | 1 | | 2 |
| <i>Combretum aculeatum</i> | | 2 | 6 | 1 | | | | | | | | | | | | | | | | | | | | | | |
| <i>C. fragans</i> | | 6 | | | | | | 1 | | | | | | | | | | | | | | | | | | |
| <i>C. glutinosum</i> | | 4 | 1 | | 1 | 1 | 1 | | | | 1 | | | | | | | | | | | | | | | |
| <i>C. molle</i> | | | 1 | | 1 | | | | | | | | | | | | | | | | | | | | | |
| <i>Commiphora africana</i> | | 3 | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| <i>C. pedunculata</i> | | 19 | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Diospyros mespiliformis</i> | | 1 | 2 | 1 | | | | | | | | | | | | | | | | | | | | | | |
| <i>Entada africana</i> | | 1 | 1 | | | | | | | | | | | | | 1 | | | | | | | | | | |
| <i>Guiera senegalensis</i> | | 3 | 3 | 2 | | | | | | | | | | | | | | | | | | | | | | |
| <i>Hoslundia opposita</i> | 1 | 47 | 31 | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Mitragyna inermis</i> | | 54 | 18 | 1 | 5 | | 1 | | | | | | | | | | | | | | | | | | | |
| <i>Pentatropis</i> sp. | | 3 | 3 | | | | | | | | | | | | | | | | | | | | | | | 3 |
| <i>Sclerocarya birrea</i> | | | | | | | | | 1 | | | 1 | 1 | | | 1 | | | | | 2 | | | | | |
| <i>Securinega virosa</i> | | | 6 | 2 | | | | | | | | | | | | | | | | | | | | | | |
| <i>Steganotaenia araliacea</i> | | 3 | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Stereospermum kunthianum</i> | | 4 | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Ziziphus mucronata</i> | | | 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 care-

fully 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-

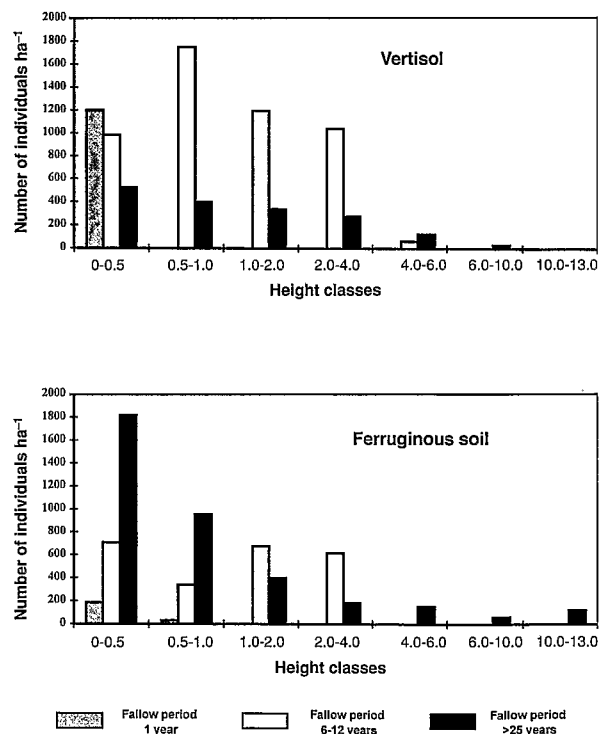


Fig. 3. Height classes of woody species on ferruginous and vertisol soil sites, after a fallow period of 1, 6-12 and >25 yr.

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 de-

struction 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.

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. Fire-

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 |

wood 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 abandonment, are progressively eliminated in the course of secondary succession. They are gradually replaced by others that are better adapted to the new conditions.

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, Seghier (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

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

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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