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# Regeneration by sprouting in slash and burn rice cultivation, Taï rain forest, Côte d'Ivoire

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ABSTRACT. In 14 forest plots (36 $m^2$) all terrestrial plant species were recorded before slashing and burning of the vegetation. During subsequent cultivation with rainfed rice all resprouting plants were registered in permanent plots (72 $m^2$). The fields studied (one per forest) covered all combinations of forest type and soil usually cultivated on local farms. Forest plots (total 409 species) and field plots (358 species) had 226 species in common. Most resprouting plants were woody. Though nine forests in the sample were secondary, 70% of resprouting plants belonged to primary forest species and with three exceptions, these species did not regenerate by seed.

Experiments in one field inlcuded: different intensities of initial burning, weeding (none, once, twice) and length of the rice cultivation period (1, 2, 3 y). Resprouting plants were monitored in permanent plots (108 $m^2$) during 3 y of cultivation and 2 y of fallow. More plants resprouted after a mild initial burning (5.8 plants $m^{-2}$) than after a burn of normal intensity (1.4 plants $m^{-2}$). Weeding and prolonged cultivation strongly reduced species diversity but plant densities were less affected because some climbers and trees were apparently stimulated and expanded.

Fields abandoned after one rice harvest had, within six months, a closed forest canopy of pioneer trees emerging from the pre-existing seed bank and from the growth of resprouting trees. Prolonged cultivation (3 y) destroyed the pre-existing seed bank but affected sprouting plants less, these being the only component in the vegetation able to shade out weeds and forbs such as *Chromolaena odorata*.

KEY WORDS: burning, *Chromolaena odorata*, Côte d'Ivoire, fallow, rainfed rice, tropical rain forest, vegetative regeneration, weeding,

## INTRODUCTION

After felling a forest, many stumps and roots produce shoots. In tropical wet forests a large part of the first woody cover which appears first after disturbance is commonly a result of coppicing stems and root stocks (Whitmore 1982, p. 281). Though the capacity of trunks and roots to develop shoots becomes progressively depleted when the land is used for agriculture, resprouting plants are still common in the fields of shifting cultivators. Regeneration back to forest is usually a combination of vegetative regrowth of pre-existing forest plants and plants grown from seed. Yet, in studies on shifting cultivation and forest regeneration, such sprouting has often been neglected. Little is known of the preval-

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ence of sprouting among tropical rain forest plants and how vegetative growth responds to fire and weeding.

In freshly cleared rain forest, the primary forest species are merely present as sprouts, contrary to secondary species and weeds which commonly develop from seed (Riswan 1979, Uhl *et al.* 1982). This vegetative regeneration makes rain forest trees and lianas not solely dependent upon seed for their reappearance after destruction of the pre-existing vegetation. Because most primary forest species have characteristically poor capacities for dispersal, resprouting forest plants provide some degree of floristic stability after disturbance (Stocker 1981, Whitmore 1983).

In forested land which has been repeatedly cleared, most of the plants are herbaceous but the woody plants present are almost all derived from stumps and root stocks (Stromgaard 1986). Rapid and efficient establishment of a woody fallow depends on there being ample coppice stumps and suckers left at the end of the period of cultivation (Ahn 1958, Clayton 1958, Kellman 1980, Lambert & Arnason 1986, Snedaker & Gamble 1969, Symington 1933). In some systems of shifting cultivation coppicing plants are protected in order to make the fallow period as short as possible (Adedeji 1984, Kushwaha *et al.* 1981, Swamy & Ramakrishnan 1988).

In successional studies dealing with coppice growth three aspects of resprouting are usually discussed: burning, the exhaustion of sprouting reserves through cultivation, and the significance of vegetative regrowth for regeneration. Some authors mention only the negative effect of fire (Maury 1979, Riswan 1979), others estimate the number of stumps and roots capable of surviving a single fire (Adedeji 1984, Kauffman 1991, Stocker 1981, Uhl *et al.* 1981). It was observed by Stocker (1981) that many trees coppiced immediately after felling, yet did not re-coppice after fire, and certain forest trees coppiced after an initial burn but subsequent fires and dry periods eliminated most. Coppice shoots become less common as agriculture intensifies, thus they are almost lacking in permanent fields (Kellman 1980). Two cycles of cultivation and repeated weeding greatly diminished the number of resprouting plants in a field (Kartawinata 1980, Uhl 1987, Whitmore 1982). Some studies compare regeneration by vegetative means with regeneration by seed (Alexandre 1989, Bormann & Likens 1979, Larpin 1989, Mitja & Hladik 1989, Stocker 1981). All conclude that coppice can rapidly cover the ground but that seedlings eventually have highest growth rates.

In this paper resprouting includes all forms of vegetative regeneration as opposed to regeneration from seed. We attempted to answer the following questions. Which part of the forest regenerates vegetatively in fields? How are resprouting plants, particularly primary forest species, affected by burning, weeding, and prolonged cultivation? Are certain functional species groups (e.g. understorey trees, lianas, ground herbs) more resistant than others? After the cultivation period, how important are resprouting plants for the recovery of the forest?

## STUDY AREA

The Taï forest in the south-western region of Côte d'Ivoire represents the largest tract of rain forest in West Africa. It forms part of the UNESCO's international network of Biosphere Reserves as well as being inscribed on the World Heritage List.

The study area (5° 57′–5° 20′ N latitude and 7° 30′–7° 14′ W longitude) receives an annual rainfall of about 1900 mm, the greater part falling in two rainy seasons. Food cultivation is performed in the heaviest rainy season, from March through August. The indigenous population, Oubi and Guéré, slash and burn mature forest with the aim to crop it with rainfed rice for one season and then let it return to forest. In this shifting cultivation system, very short cropping periods (6 months) alternate with long forest fallow periods (15–30 y). A new field is required each year. Due to population increase, widespread cocoa farming and the extension of the nearby Taï National Park, the cropping period is sometimes extended to two years and fallow periods are shortened to 6–10 y (De Rouw 1991).

The land is undulating to sloping. Rocks have weathered *in situ* to a depth of 3–20 m. The end products are severely leached, poor acid soils with kaolinite as the main clay mineral, low CEC, low organic matter content and high sesquioxide content (Development and Resources Corporation 1967, Fritsch 1980, Van Kekum 1986). Soils have been classified as ferralo-ferric acrisol (FAO/UNESCO 1974). In Table 1, analytical data from topsoil under primary forest are presented. From the hilltop to the mid slope (200–300 m) the topsoil is built up by gravelly layers to a depth of 70 cm. Over 50% of the volume consists of coarse ironstone fragments. The gravel is embedded into a red clay. Soils are well drained. From mid slope to one-third lower slope (100–150 m)

Table 1. Analytical data of topsoil under primary forest of a typical toposequence in Taï. Gravel content as percentage of whole soil, other analysis on fine earth fraction only (Fritsch 1980).

| | Depth (cm) | Crest | Upper slope | Mid slope | Lower slope | Valley bottom |
|---|---|---|---|---|---|---|
| Gravel (%) | 0–7 | 76% | 75% | 3% | 0% | 0% |
| | 7–20 | 75% | 71% | 56% | 0% | 0% |
| pH-$H_2O$ | 0–7 | 5.9 | 5.6 | 4.5 | 4.3 | 4.2 |
| | 7–20 | 4.9 | 4.7 | 4.7 | 4.4 | 4.4 |
| CEC | 0–7 | 89 | 96 | 62 | 23 | 47 |
| (m-equiv $kg^{-1}$) | 7–20 | 51 | 54 | 47 | 30 | 32 |
| Base saturation | 0–7 | 73 | 53 | 16 | 23 | 37 |
| (%) | 7–20 | 28 | 15 | 11 | 6 | 55 |
| Organic matter | 0–7 | 3.11 | 3.45 | 1.78 | 0.93 | 1.57 |
| (%) | 7–20 | 1.32 | 1.08 | 0.89 | 0.65 | 1.18 |

the gravel layers become less thick, 20–30 cm, and they are covered by 10–20 cm of sandy loam. The lower one-third of the slope (100–120 m) has sandy topsoil layers and clayey layers below. In the first 100 cm no gravel occurs. Mid slope and lower slope soils are moderately well drained. In the valley bottoms the soils are hydromorphic with clay. They show much variation in texture both vertically and horizontally (Fritsch 1980). Rice is cultivated on all soils except very gravelly crests and sandy valley bottoms; farmers, however, have a preference for mid slope positions.

The Taï National Park consists largely of untouched rain forest. Outside the Park patches of primary forest, secondary forest of different ages, fields and degraded vegetation form a mosaic. The primary forest vegetation is tropical lowland evergreen seasonal forest according to the UNESCO world classification (1973). The standing biomass varies from 350 t $ha^{-1}$ in the valley bottoms to 500 t $ha^{-1}$ on the slopes (Huttel 1977). Primary forest vegetation has been studied by Guillaumet (1967), secondary forest by Alexandre *et al.* (1978), Kahn (1982), Jaffre & De Namur (1983). A synthesis of the work on the Taï forest ecosystem has been published (Guillaumet *et al.* 1984). The natural resources, including lithology, soils, undisturbed forest vegetation and human-modified vegetation as well as land uses, have been described and mapped recently (De Rouw *et al.* 1990).

## METHODS

Vegetative regrowth was studied through permanent plots in the fields (N = 14) of local farmers. The main differences between fields were related to topographic position and type of forest cleared: primary forest (fields 10, 11, 12, 13, 14), secondary forest, either old (field 6, 30 y, field 3, 21 y, field 4, 20 y, field 1, 19 y, field 7, 16 y, field 8, 15 y, field 9, 14 y), or young (fields 2 and 5 both 6 y). Two fields (6, 11) were situated at the upper slope, four fields at mid slope (1, 2, 8, 9), five fields at lower slope (3, 4, 12, 13, 14), and three in valley bottoms (5, 7, 10). Sites of 1 ha were surveyed before clearing: the soil by auguring down to 120 cm and the vegetation by making releves. A list of plant species was made after examination of all terrestrial plants in two plots of 18 $m^2$. All forest sites were felled and burnt and the field cultivated with rice following the local practice. All vegetation was cut close to the ground except for trees with a girth over about 20 cm which were felled well above the ground where it was easier to use force. One burning was made at the end of the relative dry season. Burning, however, is never complete because those places with too thin a layer of trash or patches covered by moist material, especially at field margins, are often only slightly burnt. In each field four permanent plots (each 18 $m^2$) were laid out in areas where burning had been normal. In these plots all plants were identified and counted and a distinction was made between seedlings and vegetative regrowth. Often the plants had to be pulled out or the soil around them had to be removed in order to check the method of regeneration. Such surveys were made 3 months (weeding of the field), 5 months (harvest of the rice), and 12 months after the burn.

Field 1 was used for detailed studies. About 5% of the surface had received only a mild fire. Normally burnt areas had charred trunks, branches and stumps and showed other visible traces of fire such as charcoal and white ash on the soil surface. Slightly burnt areas were characterized by the absence of the above-mentioned features and by the presence of twigs. The rice was sown (dibbled) a few days after the burn. In the experiment two factors were investigated: intensity of burning, normal or slight, and weeding frequency, no weeding, one weeding (3 months after the burn), and two weedings (2 and 3 months after the burn). Plots were single-replicate units of 9 $m^2$. Observations on rice (yield and yield components), weeds grown from seed (species, number of plants, height, cover, biomass), and resprouting plants (species, number of plants, height, cover, biomass, number of shoots produced) were made 2, 3 and 5 months after the burn. Biomass was determined from seedlings which were pulled out and from shoots which were cut off.

Half the field, including all the permanent plots was re-cropped with rice in the following rainy season. Slashing and burning preceded this second crop. Observations in the plots were a repetition of the previous year and each plot kept the same frequency of weeding. A third rice crop was sown the next year in part of the field that included the permanent plots. Observations on rice and weeds were consistent with those of the previous years but no biomass was determined. After the third rice harvest the field was left as such. The permanent plots were surveyed after one and two years of fallow. At the end of the experiment a final survey was made in the vegetation that had developed after one rice crop and four years of fallow (2 plots of 18 $m^2$) and in the regrowth that had sprung up after two rice crops and three years of fallow (2 plots of 18 $m^2$). These surveys in fallow vegetation included identification of all plant species, cover and height, regeneration by and sprouting of by seed. Chemical analysis of topsoil (0–10 cm) was made once a year in each plot.

## RESULTS

### *Resprouting forest species*

The average number of species in the fourteen forest plots was 68 (36 $m^2$) and after slashing and burning a mean of 63 resprouting species was found in field plots (72 $m^2$). About 50 species, most of them sprouts and occurring once or twice in the survey, could not be identified to species. The older the cleared forest, the greater the floristic variation among resprouting plants. Fields made in primary forest were particularly rich, but swamp forest on the contrary, was exceptionally poor in species. This could be due to the extreme change in micro-climate when swamp forest is cleared for agriculture.

In Table 2 total numbers of identified species in forest and in the fields are presented. A differentiation according to life form has been made. The special

Table 2. Number of species according to life form recorded in 14 forests (Taï) before slashing and burning of the vegetation and number of species resprouting from vegetative parts during subsequent cultivation (i.e. in 14 fields). Forest was sampled in 36 $m^2$ plots, rice fields in permanent plots (72 $m^2$) 3, 5 and 12 months after burning.

| | Number of species in forest plots | Number of species resprouting in fields | % primary forest species resprouting in fields | Number of species both in forest and field | Genera common in field |
|---|---|---|---|---|---|
| Large trees >30 m | 31 | 36 | 44 | 15 | |
| Medium-sized trees 5–30 m | 92 | 76 | 59 | 52 | |
| Small trees 1.5–5 m | 56 | 47 | 81 | 32 | |
| Special groups | | | | | |
| Pygmy trees <1.5 m | 19 | 15 | 100 | 10 | |
| Unbranched trees | 9 | 7 | 100 | 3 | *Tricoscypha* (4 spp) |
| Erect palms | 2 | 0 | — | 0 | |
| Large climbers >30 m | 19 | 20 | 100 | 15 | |
| Medium-sized climbers 5–30 m | 49 | 63 | 75 | 37 | *Combretum*, *Salacia* (8 spp) |
| Small woody climbers <5 m | 33 | 27 | 59 | 15 | *Clerodendrum* (4 spp) |
| Herbaceous climbers | 23 | 17 | 35 | 12 | *Dioscorea* (5 spp) |
| Special groups | | | | | |
| Climbing palms | 4 | 2 | 100 | 2 | |
| Ground herbs | 34 | 30 | 83 | 20 | *Aframomum* (7 spp), *Costus* (5 spp) |
| Special groups | | | | | |
| Grasses | 8 | 4 | 0 | 3 | |
| Cyperaceae | 2 | 1 | 100 | 1 | |
| Araceae | 13 | 11 | 91 | 8 | *Culcasia* (7 spp) |
| Ferns | 15 | 2 | 50 | 1 | |

groups, pygmy trees, unbranched trees, etc. (except grasses), were set apart because they constitute typical features of primary forest in Taï (Guillaumet 1967). Plant nomenclature follows Hutchinson & Dalziel (1954–1968) and Knecht (1983) for Araceae, Hallé (1962) for Celastraceae.

Many of the large and medium-sized trees which coppiced in fields belonged to secondary forest species. This is due to the fact that 9 out of 14 forests had a canopy built up by secondary forest trees, while the understorey was already colonized by primary forest growth. Primary forest species accounted for 70% of resprouting plants, only three species: *Geophila obvallata*, *Microdesmis puberula* and *Dialium aubrevillei* also regenerated from seed. In Table 3 an enumeration of all species occurring more than seven times in fields or forests is given. The abundance of medium-sized lianas in field plots (Tables 2, 3) is probably the result of a number of them having been 'missed' in forest plots. Leafless liana stems could not be identified in most cases. Resprouting plants belonged to 71 families, Rubiaceae (33 spp) being the most common one. Other families well represented were: Euphorbiaceae (18 spp), Papilionaceae and Apocynaceae (15 spp), Caesalpineaceae and Celastraceae (14 spp). These families were the most prominent in forest plots too. Zingiberaceae in fields (12 spp) were less represented in forest (5 spp), as were the families with many lianas (Combretaceae and Connaraceae, both 11 spp).

### *Resistance to slashing, burning and weeding*

*Species.* In the permanent plots of field 1 (12 plots of 9 m$^2$), those plants regenerating vegetatively belonged to 153 different species, against 201 different species growing from seed. Only 45 plant species sprouted and regenerated from seed equally. Figure 1 shows the decline of number of resprouting species in these permanent plots as well as the total number of species observed in the plots.

The close observation of resprouting plants allowed estimation of the time of exhaustion. Figure 2 shows the gradual disappearance of sprouting plant species suffering the consequences of repeated clearance and the competition with the fallow vegetation. Plots where the initial burning had been slight were floristically richer than normally burnt plots. This difference was prominent during the first year of cultivation but declined in subsequent years of cultivation and levelled out during the two years of fallow. Most species (76%) present in the normally burnt plots were represented in the mildly burnt plots. Herbaceous species were less resistant to burning and prolonged cultivation. Plants belonging to the same species tended to disappear from the field at about the same time after having received similar treatment. In Table 4 the coppicing plant species represented in the plots by three or more individuals are arranged according to resistance to clearing and competition. A distinction has been made between plant species only regenerating by sprouting, and species, constituting a much smaller group, present both as sprouts and seedlings. The first

Table 3. Occurrences of species in forest vegetation shortly before clearing and as resprouting plants after slashing and burning (Taï). Total of 14 forests (then fields) were sampled: plots 36 m² in forest, 72 m² permanent plots in fields surveyed 3, 5 and 12 months after burning.

| | Species | Family | Number of occurrences in forests | fields |
|---|---|---|---|---|
| **Common in forest and field** | | | | |
| Trees | *Baphia bancoensis* | Papilionaceae | 5 | 8 |
| | *Cola heterophylla* | Sterculiaceae | 7 | 4 |
| | *Dialium aubrevillei* | Caesalpiniaceae | 7 | 4 |
| | *Diospyros soubreana* | Ebenaceae | 7 | 4 |
| | *Ficus capensis* | Moraceae | 4 | 9 |
| | *Hunteria simii* | Apocynaceae | 10 | 6 |
| | *Hymenostegia afzelii* | Caesalpiniaceae | 7 | 4 |
| | *Microdesmis puberula* | Euphorbiaceae | 8 | 10 |
| | *Myrianthus libericus* | Moraceae | 3 | 7 |
| | *Napoleona leonensis* | Lecythidaceae | 10 | 11 |
| | *Rauvolfia vomitoria* | Apocynaceae | 4 | 9 |
| | *Strombosia glaucescens* | Olacaceae | 8 | 7 |
| Climbers | *Agelaea trifolia* | Connaraceae | 5 | 9 |
| | *Ancistrophyllum secundiflorum* | Palmae | 5 | 7 |
| | *Calycobolus africanus* | Convolvulaceae | 7 | 4 |
| | *Cercestis afzelii* | Araceae | 10 | 6 |
| | *Cnestis ferruginea* | Connaraceae | 6 | 9 |
| | *Dioscorea burkilliana* | Dioscoreaceae | 4 | 8 |
| | *Griffonia simplicifolia* | Caesalpiniaceae | 8 | 11 |
| | *Hypselodelphys violacea* | Marantaceae | 6 | 8 |
| | *Manniophyton fulvum* | Euphorbiaceae | 5 | 7 |
| | *Pyrenacantha vogeliana* | Icacinaceae | 5 | 10 |
| | *Rhaphiostylis beninensis* | Icacinaceae | 7 | 9 |
| | *Tiliacora dinklagei* | Menispermaceae | 10 | 7 |
| Ground herbs | *Geophila obvallata* | Rubiaceae | 8 | 14 |
| **More in forest than in field** | | | | |
| Trees | *Chrysophyllum taiense* | Sapotaceae | 7 | 1 |
| | *Diospyros mannii* | Ebenaceae | 8 | 1 |
| | *Ptychopetalum anceps* | Olacaceae | 7 | 2 |
| | *Trichilia heudelotii* | Meliaceae | 7 | 2 |
| Climbers | *Piper guineense* | Piperaceae | 7 | 2 |
| **More in field than in forest** | | | | |
| Trees | *Rinorea longicuspis* | Violaceae | 2 | 7 |
| Climbers | *Clerodendrum volubile* | Verbenaceae | 2 | 9 |
| | *Clerodendrum splendens* | Verbenaceae | 0 | 10 |
| | *Dichapetalum pallidum* | Chailletiaceae | 1 | 7 |
| | *Dioscorea praehensilis* | Diocoreaceae | 2 | 7 |
| | *Platycepalum hirsutum* | Papilionaceae | 1 | 10 |
| Ground herbs | *Costus afer* | Zingiberaceae | 1 | 8 |

Full species list can be obtained from the author.

group disappears from the field or fallow vegetation with the death of the vegetative plant, while the latter has a chance to remain in the vegetation because it can establish from seed. It was confirmed by the data from the other fields that those species regenerating by sprouting, by seed, and those capable of both modes of regeneration, form distinct groups. Among all species identified, 406 occurred only as resprouting plants, 347 only as seedlings, while 542 species could do both.

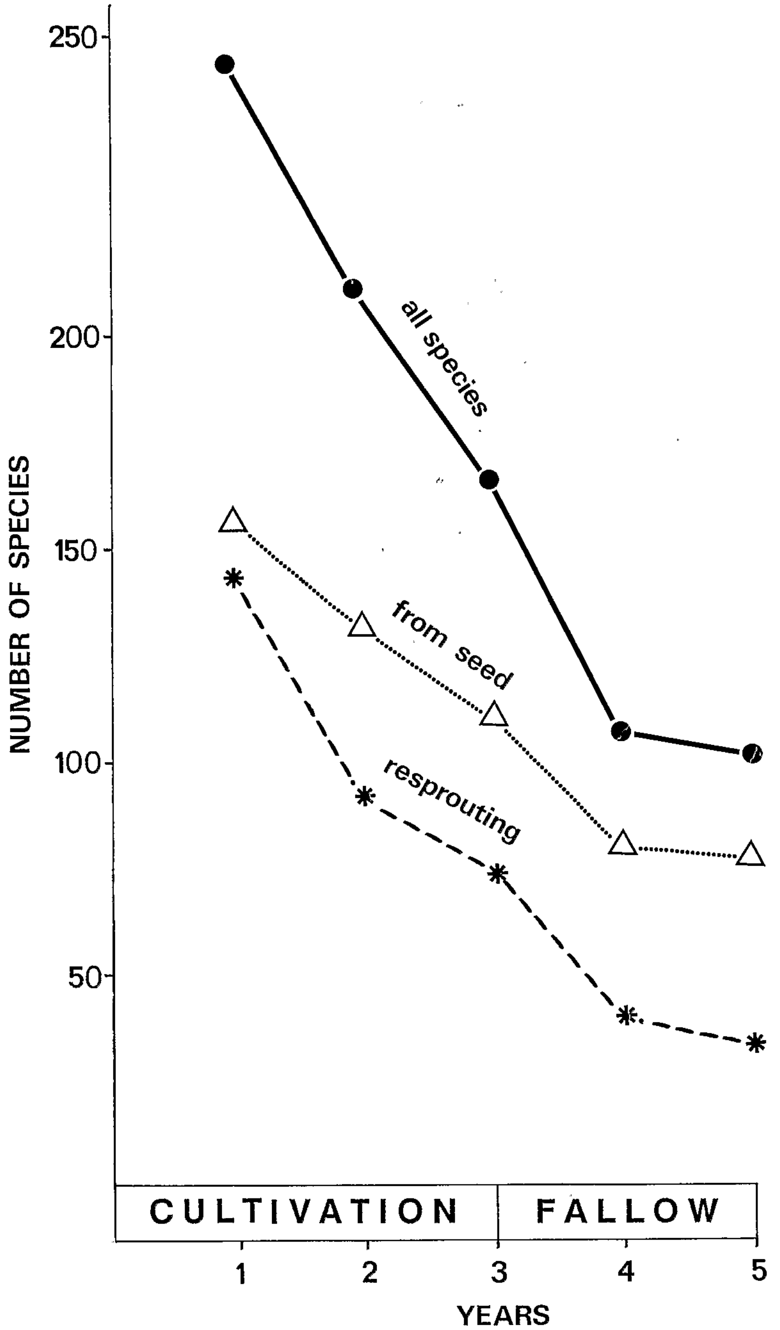


Figure 1. The number of species established from seed and resprouting from the pre-existing forest present in permanent plots ($12 \times 9$ m$^2$) in field 1 during three years of cultivation and two years of subsequent fallow (Taï forest).

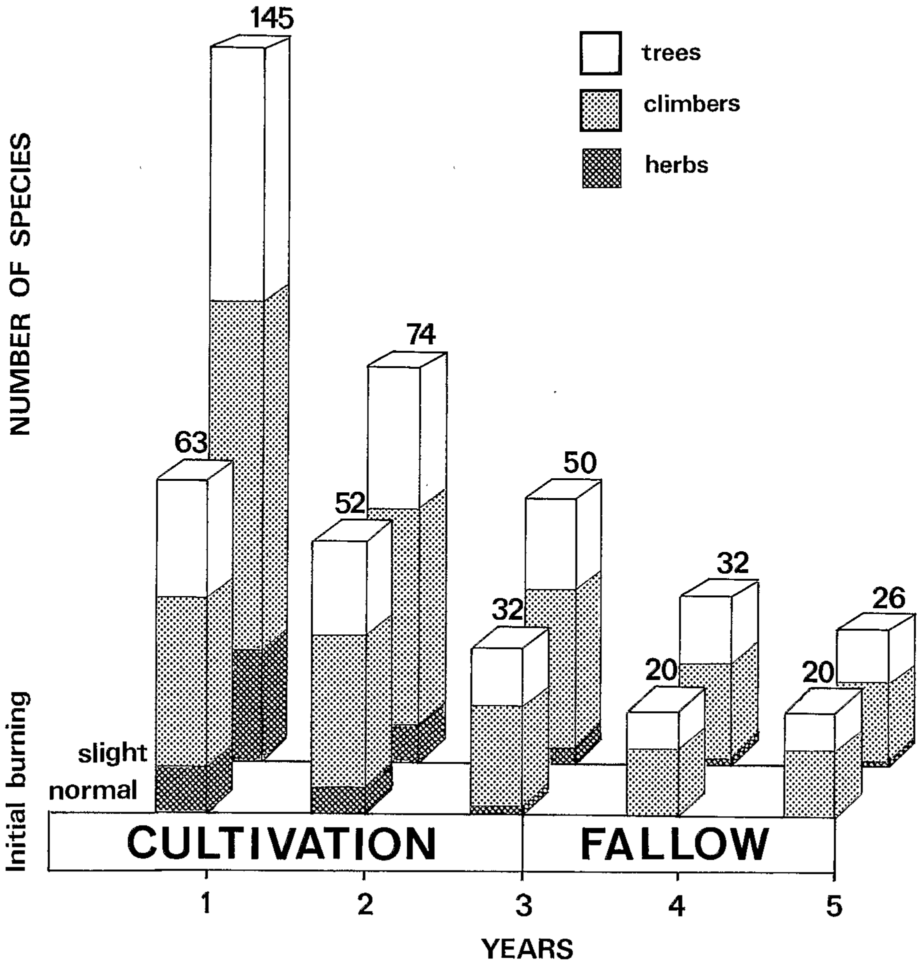


Figure 2. The numbers of tree, climber, and herbaceous species resprouting during years of cultivation and fallow in field 1, Taï forest. Observations were made in permanent plots (6 × 9 m²) where the initial burning had been normal, and where the initial burning had been slight (6 × 9 m²).

Many primary forest species, mostly understorey plants, were present as one or two individuals in the permanent plots. During the first year they produced one or two sprouts and then disappeared. Other plants survived three years of cultivation but disappeared once the field was left to itself. Plants still producing sprouts five years after the felling of the forest, not only survived repeated slashing, burning and weeding, but also were successful competitors once the field was invaded by a fallow vegetation.

In the first year of cultivation, 50% of the sprouting plants in the normally burnt plots belonged to primary forest species, increasing to 61% and 60% in the second and third year. In the slightly burnt plots, this was 61% the first year, decreasing to 59% and 51% in the following two years. During the two

Table 4. Number of years that plant species of the pre-existing secondary forest resprout during rice cultivation and fallowing (Taï). (*species that survived only a mild initial burning, LT large tree, MT medium-sized tree, ST small tree, PT pygmy tree, LC large climber, SC small woody climber, HC herbaceous climber, CP climbing palm, GH ground herb, FE fern.)

| | Regeneration only by sprouting | Regeneration by sprouting and by seed |
|---|---|---|
| Species resprout during 1 year of cultivation, then die | *Cephaëlis peduncularis* (PT)<br>**Chrysophyllum taïense* (MT)<br>**Distemonanthus benthamianus* (MT)<br>**Geophila afzelii* (GH)<br>**Lovoa trichilioides* (LT)<br>*Mareya micrantha* (MT)<br>**Myrianthus libericus* (MT)<br>**Palisota hirsuta* (GH)<br>**Sarcophrynium brachystachys* (GH) | *Aframomum daniellii* (GH)<br>*Aframomum sceptrum* (GH)<br>**Afrosersalisia afzelii* (LT)<br>**Albizia zygia* (MT)<br>*Alchornea cordifolia* (MT)<br>*Ampelocissus gracilipes* (HC)<br>**Dialium aubrevillei* (LT)<br>**Dioscorea bulbifera* (HC)<br>**Dioscorea liebrechtsiana* (MC-HC)<br>**Dioscorea minutiflora* (HC)<br>**Dioscorea smilacifolia* (HC)<br>*Fagara macrophylla* (MT)<br>*Marantochloa congensis* (GH)<br>**Piptadeniastrum africanum* (LT)<br>**Trichilia heudelotii* (MT) |
| Species resprout during 2 years of cultivation, then die | *Ancistrophyllum secundiflorum* (CP)<br>*Bequaertia mucronata* (SC)<br>*Blighia welwitschii* (MT)<br>*Calpocalyx brevibracteatus* (MT)<br>*Clerodendrum splendens* (SC)<br>**Combretum aphanopetalum* (MC)<br>*Erytrococca anomala* (ST)<br>*Myrianthus arboreus* (MT)<br>**Neuropeltis acuminata* (LC)<br>*Platysepalum hirsutum* (LC)<br>*Secamone afzelii* (MC)<br>*Sterculia tragacantha* (MT) | *Albizia adianthifolia* (MT)<br>*Chlorophytum orchidastrum* (GH)<br>*Costus deistelii* (GH)<br>*Dioscorea burkilliana* (HC)<br>*Megaphrynium macrostachyum* (GH) |
| Species resprout during 3 years of cultivation, then die | **Anchomanes difformis* (AR)<br>**Combretum dolichopetalum* (MC)<br>*Combretum homalioides* (MC)<br>*Combretum paniculatum* (MC)<br>**Combretum platypterum* (MC)<br>*Monodora tenuifolia* (MT)<br>*Pteris burtoni* (FE)<br>*Rinorea longicuspis* (ST)<br>*Salacia debilis* (MC)<br>*Salacia erecta* (MC) | *Dioscorea praehensilis* (MC-HC)<br>*Phyllanthus discoideus* (MT)<br>*Rauvolfia vomitoria* (MT) |
| Species resprout during 3 years of cultivation and 1 year of fallow, then die | **Agelaea trifolia* (LC)<br>*Canthium multiflorum* (SC)<br>*Combretum grandiflorum* (MC)<br>**Loeseneriella africana* (SC) | |
| Species resprout during 3 years of cultivation and 2 years of fallow | *Baphia bancoensis* (MT)<br>*Clerodendrum schweinfurthii* (ST)<br>*Clerodendrum volubile* (SC)<br>*Cnestis ferruginea* (MC)<br>**Euadenia trifoliolata* (PT)<br>*Griffonia simplicifolia* (MC)<br>*Hippocratea pallens* (MC)<br>*Ipomoea mauritiana* (HC)<br>*Leptoderris miegei* (MC)<br>*Millettia zechiana* (ST)<br>*Napoleona leonensis* (ST)<br>*Pyrenacantha vogeliana* (SC)<br>**Salacia calumna* (SC) | *Dioscorea preussii* (HC)<br>*Ficus capensis* (MT)<br>*Geophila obvallata* (GH)<br>*Mezoneuron benthamianum* (SC)<br>**Microdesmis puberula* (ST)<br>*Mildbraedia paniculata* (PT) |

years of fallow this high percentage of primary forest species was maintained. So those primary forest species surviving initial land clearing were no less resistant to disturbance than secondary forest species. A total of 54 coppicing secondary forest species and 99 primary forest species was identified in the plots.

*Plant densities.* Plant density was also strongly affected by the intensity of the initial burning and there was a marked response to weeding frequency (Figure 3). During the first and the second year of cultivation differences in resprouting plant densities in the plots were mainly a result of variations in fire intensities generated by the initial burning. In the slightly burnt plots two cultivation cycles and weeding reduced the plant densities to 1.3 plants $m^{-2}$, whereas cultivation during three seasons and no weeding brought densities down to about

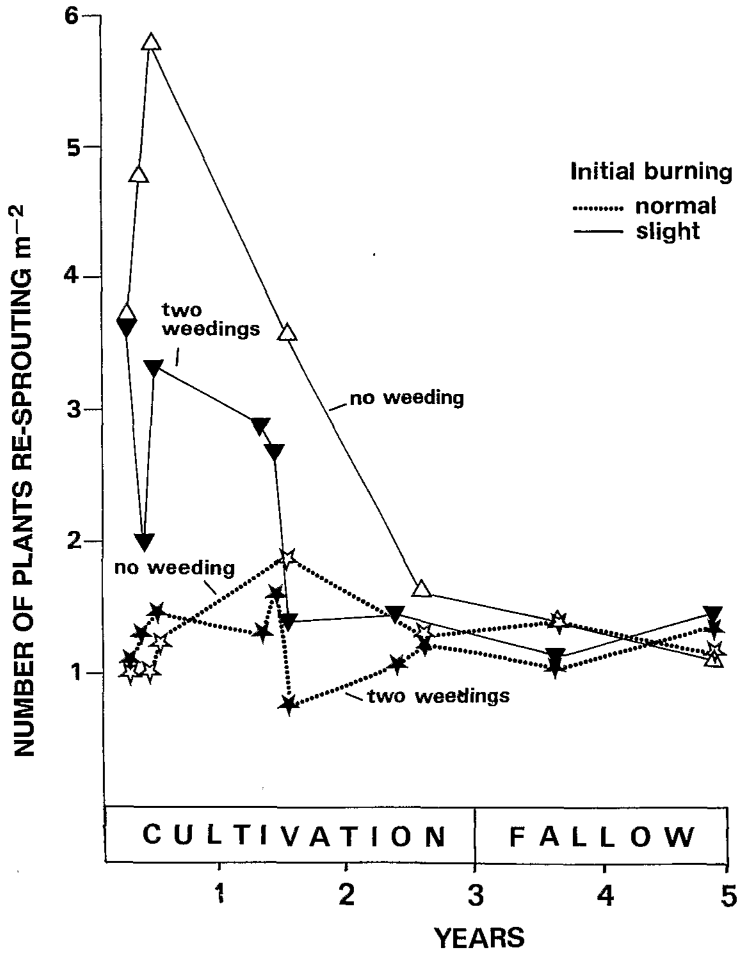


Figure 3. The densities of resprouting plants during three years of cultivation and two years of fallow in permanent plots where the initial burning had been normal or slight. No weeding is compared with two weedings (field 1, Taï forest).

the same level. Here, weeding strongly reduced plant densities during the first cultivation year, in contrast with the normally burnt plots where plant densities were less affected by weeding. Apparently plants surviving a normal initial burn can overcome repeated weeding as well, but plants able to survive only a mild burning succumb to subsequent weeding. In the following years, however, weeding killed off resprouting plants both in the normally and in the slightly burnt plots so that plant densities stabilized at 1.0–1.4 sprouting plants $m^{-2}$ independent of treatment. This level was maintained during the following two years of fallowing.

Among the primary and secondary forest species a similar tendency could be observed over the years: a decrease in herbaceous plants and an increase in the contribution made by climbers. In the normally burnt plots the number of herbaceous plants diminished from 10 to 1% (from 26 to 5% in the slightly burnt plots), and the proportion of climbers increased from 18% the first year of cultivation to 75% five years later (from 25 and 70% respectively in the slightly burnt plots).

Average densities of resprouting plants in plots on the 13 other fields investigated ranged from 0.58 plants $m^{-2}$ to 1.97 plants $m^{-2}$ (mean 1.28 SD 0.385). Fields made in primary forest were no different from those prepared in secondary forest, nor did it matter whether the last fallow period had been long, over 16 y, or short, 6 y. No significant relation could be detected between density of resprouting plants and topographic position. There was only a relation between number of herbaceous plants and position on the slope, opposing fields in valley bottoms to fields on higher positions. In valley bottoms up to 40% of sprouting plants consisted of non-woody plants (Marantaceae and Zingiberaceae), compared with a maximum of 20% in fields on slopes.

*Number of shoots produced.* Resprouting plants can be rated by their number of shoots produced simultaneously. This was not so much a characteristic of species but depended more on the size of the plant and on the extent to which the plant had suffered from initial burning. Large plants produced more shoots than smaller ones, independent of the treatment. Plants of the same species could sprout with a double amount of shoots in the slightly burnt plots. On normally burnt places most sprouts grew from buried buds, on slightly burnt places buds situated above the ground could also develop.

In the first year of cultivation, the number of shoots per plant was approximately the same for all treatments (Table 5). This means, firstly, that the greater number of shoots present in the slightly burnt plots was a result of a superior number of resprouting plants present there, and not of a greater number of shoots per plant, and secondly, that weeding was a major reason for the death of the plants. In the normally burnt plots, during the second year of cultivation, the average number of shoots per plant had doubled. Weeding reduced the number of resprouting plants by eliminating preferably those plants sprouting with few shoots. Among the surviving plants, those with a high sprout number

Table 5. Number of shoots per plant and total number of shoots (mean of 2 plots, each 9 m² at the end of each cropping cycle (Taï forest).

| | 1st year | | 2nd year | | 3rd year | |
|---|---|---|---|---|---|---|
| | Shoots per plant | Total shoots | Shoots per plant | Total shoots | Shoots per plant | Total shoots |
| Normal initial burning | | | | | | |
| No weeding | 4.3 | 98 | 7.8 | 266 | 2.5 | 59 |
| Two weedings | 3.2 | 84 | 8.6 | 112 | 9.0 | 117 |
| Slight initial burning | | | | | | |
| No weeding | 4.5 | 409 | 4.3 | 267 | 2.6 | 73 |
| Two weedings | 5.3 | 282 | 4.7 | 94 | 5.9 | 134 |

had resisted. In the slightly burnt plots the average number of sprouts per plant remained the same, compared to the previous year but the number of sprouting plants was further reduced by weeding. During the third cultivation year an important difference was found between the weeded and the unweeded plots, both in the normally and in the slightly burnt plots. Those plants still persisting not only resisted repeated clearing of the field, but were apparently stimulated by weeding. Freed from competition for a while, they expanded and produced a large number of shoots.

In some cases the number of sprouts produced per individual can be a species characteristic as some species always produced many more sprouts than average. Only a few species produced more than 20 sprouts per plant after each disturbance: the lianas *Tetracera potatoria*, *Campylostemon* sp, *Griffonia simplicifolia*, *Hippocratea pallens*, *Secamone afzelii*, and the trees, *Sterculia tragacantha*, *Calpocalyx brevibracteolatus*, *Baphia bancoensis*, *Ficus capensis*. The understorey shrub *Microdesmis puberula* resprouted most abundantly of all.

*Rhythm of shoot production.* The rhythm of shoot production proved largely a species attribute, though size of the plant and environmental factors may have played a role. A large group of species sprouted promptly after each cutting, and, once a plant failed to appear, it had very probably died (*Ancistrophyllum secundiflorum*, *Baphia bancoensis*, *Canthium multiflorum*, *Cnestis ferruginea*, *Combretum homalioides*, *Griffonia simplicifolia*, *Hippocratea pallens*, *Myrianthus arboreus*, *Rothmannia longiflora*, *Microdesmis puberula*). Another group comprised plant species not found at each recording. They seemed to take longer to recover or did not resprout during the drier season, or in full sunlight. Before they succumbed, appearances became less and less frequent (*Clerodendrum splendens*, *Clerodendrum schweinfurthii*, *Dalbergia albiflora*, *Dioscorea bulbifera*, *Dioscorea preusii*, *Fagara macrophylla*, *Leptoderris miegei*, *Monodora tenuifolia*, *Secamone afzelii*, *Uvaria ovata*, *Vitex thyrsiflora*). An extreme example was the pygmy tree *Euadenia trifoliolata*, known in the local language as 'witch plant'. It sprouted with one or two conspicuous spotted leaves, then disappeared for years to reappear unexpectedly.

*Dynamics of the field and fallow vegetation*

*Biomass.* Above-ground dry weight of weeds was determined at each weeding and at the rice harvest. A distinction was made between: regeneration by germination of seeds, regeneration by sprouting of plants present prior to first cutting and burning, and regeneration by 'pseudo-coppice', i.e. germination of seeds during the first cultivation year, followed by firm establishment of the plant; during the second (and third) cultivation year the plant regenerates by sprouting.

In Table 6 dry weights of weeds are presented according to these regeneration categories. In the normally burnt plots dry weight of rice straw and paddy accounted for about 400 gm $m^{-2}$ in the weeded plots and 250 gm $m^{-2}$ in the unweeded plots. Dry paddy yield was slightly better in the weeded plots (1.5 t $ha^{-1}$) than in the unweeded plots (1.3 t $ha^{-1}$). In the slightly burnt plots rice grew poorly, producing less than 0.1 t $ha^{-1}$ paddy and about 50 gm $m^{-2}$ biomass independently of weeding. Lack of fertilizing ashes together with acid soil seemed to have reduced the performances of weeds too. Although almost six times as many sprouting plants were present, less than twice the biomass was produced. In the second year of cultivation the biomass produced by sprouts and seedlings increased, whereas biomass produced by the rice crop dropped to less than 50 gm $m^{-2}$. Paddy yield was below 0.1 t $ha^{-1}$ in both weeded and unweeded plots. The group of plants regenerating by means of 'pseudo-coppice',

Table 6. Weed biomass produced (g dry weight $m^{-2}$) during the cropping period by plants of three regeneration groups, Taï forest (see text).

| | Two weedings | | | No weeding |
|---|---|---|---|---|
| Time period (months) | 0–2 | 2–3 | 3–5 | 0–5 |
| **First year of cultivation** | | | | |
| Normal initial burning | | | | |
| sprouts | 1.5 | 3.0 | 3.3 | 26.9 |
| seedlings | 5.8 | 0.9 | 0.9 | 91.7 |
| Slight initial burning | | | | |
| sprouts | 9.0 | 2.5 | 5.9 | 42.2 |
| seedlings | 10.5 | 2.3 | 2.3 | 59.3 |
| **Second year of cultivation** | | | | |
| Normal initial burning | | | | |
| sprouts | 4.7 | ND | 13.6 | 45.3 |
| seedlings | 27.2 | ND | 46.8 | 248.7 |
| pseudo-coppice | 1.4 | ND | 1.9 | 53.4 |
| Slight initial burning | | | | |
| sprouts | 11.7 | ND | 8.6 | 64.2 |
| seedlings | 23.3 | ND | 0.5 | 177.8 |
| pseudo-coppice | 2.5 | ND | 0.5 | 7.0 |

ND = no data

mainly present in the normally burnt plots (4–8 plants $m^{-2}$), contained many sub-woody plants of the genus *Solanum* and some pioneer trees, *Harungana madagascarienis* and *Phyllanthus discoideus*. They recovered less rapidly from weeding than sprouting plants. *Solanum verbascifolium*, having a strong taproot and *Chromolaena odorata* (L.) King & Robinson, were most successful.

*Development of the fallow vegetation.* During the first year of cultivation the weed population consisted of many woody plants, mainly pioneer trees grown from seed. Weeding reduced the number of seedlings effectively but did not influence the percentage of woody plants in the population (Table 7). The superior densities of weeds observed in the slightly burnt plots were apparently a result of more seeds having remained viable after the initial burn.

Six months after the rice harvest in that part of the field abandoned after one rice crop, pioneer trees grew along with coppicing tree stumps forming a closed canopy 2–4 m above the ground. Climbing heliophyl herbs and resprouting lianas were part of the canopy too (*Dioscorea* spp, *Adenia* spp, *Combretum* spp). By that time the non-climbing arable weeds developed from seed had completed their life cycle and only some weeds of shady places persisted. During the following three years, the vegetation gained height but changed little floristically. Most trees grown from seed (*Macaranga* spp, *Musanga cecropioides*) succeeded in overtopping trees developed vegetatively from coppice. Depending on the number of resprouting plants, plots were rather species-rich, (40–80 species, 18

Table 7. Total number of individuals $m^{-2}$ at the end of each cropping period and number of woody plants by different means of regeneration, burning intensity and weeding frequency (Taï forest).

| | Initial burning normal | | Initial burning slight | |
|---|---|---|---|---|
| | Two weedings | No weeding | Two weedings | No weeding |
| **First year of cultivation** | | | | |
| Total weeds | 18.2 | 56.8 | 53.1 | 75.3 |
| Woody plants | | | | |
| from seed | 5.4 | 17.3 | 23.7 | 28.4 |
| from coppice | 0.8 | 0.9 | 2.7 | 3.9 |
| **Second year of cultivation** | | | | |
| Total weeds | 49.4 | 126.3 | 20.5 | 68.0 |
| Woody plants | | | | |
| from seed | 0.0 | 0.4 | 2.0 | 4.3 |
| from coppice | 0.4 | 1.1 | 0.6 | 2.5 |
| from pseudo-coppice | 0.1 | 0.3 | 0.0 | 0.8 |
| **Third year of cultivation** | | | | |
| Total weeds | 29.4 | 54.0 | 118.0 | 146.5 |
| Woody plants | 0.5 | 0.1 | 4.6 | 2.2 |
| from seed | | | | |
| from coppice | 0.9 | 1.1 | 1.1 | 1.5 |
| from pseudo-coppice | 0.0 | 0.1 | 18.5 | 6.3 |

m$^{-2}$). The rapid development of a forest cover was assured by pioneer trees, though coppicing trees and lianas probably assisted by shading out the weeds. No grasses were recorded.

Densities of arable weeds increased in the second year of cultivation, whereas woody plants established from seed almost disappeared (Table 7). The sub-woody forb *Chromolaena odorata* had invaded massively and heliophyl grasses (*Panicum laxum*, *Paspalum conjugatum*) appeared. The majority of these weeds produced fruits continuously, *Chromolaena odorata* spread both by seed and vegetatively. In the absence of shade, seeds germinated in every place opened up. In that part of the field abandoned after two years of cultivation, *Chromolaena odorata* formed a solid thicket about 3 m high a few months after the last rice harvest. This forb rapidly out-competed grasses and low weeds. During the following three years of undisturbed growth, succession to a forest-like structure was dependent on the presence and number of trees and lianas capable of piercing the thicket canopy. This overhead shade was produced mostly by coppicing trees (*Sterculia tragacantha*, *Ficus* spp) and lianas either resprouting from stumps or grown from seed. These plants, frequently established before the cultivation period, climbed to the upper layer of the thicket canopy. As a result, *Chromolaena odorata* degenerated and some succession could be observed towards a forest fallow. On sites where no such plants were available, *Chromolaena odorata* remained dominant throughout the remaining three years of the experiment. Very few seedlings of other plant species managed to germinate underneath. Species richness, too, was dependent on the position held by *Chromolaena odorata*, varying between 15 and 30 species in plots of 18 m$^2$.

During the third cropping year a differentiation took place according to weeding. At the moment of abandonment the weeded plots where initial burning had been normal were covered by a low, grassy layer with some shrubby coppice growth and a few *Chromolaena odorata* plants. Apparently, *Chromolaena odorata* could not expand sufficiently rapidly after each weeding to suppress grasses. In the unweeded plots, *Chromolaena odorata* dominated the grasses and about the same number of shrubs occurred. In the slightly burnt plots, independently of weeding, resprouting lianas and shrubs covered most of the ground suppressing grasses and *Chromolaena odorata* as in the weeded plots. During the following two years of fallow, some signs of succession could be observed in the weeded plots infested by grasses, though they were not completely driven out. Their position was weakened by the light shade produced by sprouting plants and by *Chromolaena odorata*. In places with moderate grass cover, the unweeded plots, *Chromolaena odorata* spread, both from seed and pseudo-coppice, and suppressed the plants of all other groups. In the slightly burnt plots, with few grasses present, *Chromolaena odorata* developed in competition mainly with sprouting plants, lianas and scandent shrubs that used the forb as a support. After two years this vegetation was no different from that developed after two years of cultivation and three years of regrowth.

## DISCUSSION AND CONCLUSIONS

We expect that all plants regenerating by sprouting in a field were once part of the pre-existing forest. The stems of trees and climbers had been cut off and the above-ground parts of herbs were destroyed by the fire. Possible exceptions are plants capable of forming storage tissue, bulbs, bulbils, corms and tuberous stems and roots. These plants might not have been present in the forest as green plants but dormant in or at the surface of the soil. This possibility would explain the absence or low frequency of *Dioscorea* spp, *Dioscoreoplyllum* spp, *Smilax kraussiana*, *Secamone afzelii* and *Anchomanes difformis* in forest plots and their abundance as sprouting plants in fields. Hladik (pers. comm.) observed in Gabon that *Dioscorea* tubers remained dormant for an indeterminate period in rain forest to grow out in gaps when light conditions were better. Regrowth of the vegetation after disturbance arises from three pools (Alexandre 1989, Bormann & Likens 1979): regeneration by sprouting of plants present prior to cutting and burning, regeneration by seeds from the forest seed bank, and regeneration by seeds transported to the site. It would be interesting to consider a fourth possibility: a bank of vegetative reproduction structures. The existence of storage structures is sometimes indicated (*Dioscoreophyllum* spp, Sommerfield 1977, *Secamone afzelii*, *Anchomanes difformis* Jaeger & Adams 1980, *Smilax*, *Haemanthus* and others, Hutchinson & Dalziel 1954–1972), whereas little is known of how they function.

Uhl (1980) gives densities for resprouting woody plants three months after cutting the forest of 6.37 plants $m^{-2}$. Four months after burning this is reduced to 0.63 plants $m^{-2}$. Repeated weeding (without burning) at least five times in two and a half years that followed, was held responsible for the exhaustion of sprouting reserves, expressed in a steady decline of plant densities to about 0.11 individuals $m^{-2}$ (Uhl *et al.* 1982). In the data provided by Uhl (1980), densities prior to burning are comparable to the Taï data on the slightly burnt plots, but data from subsequently burnt and weeded plots are far below those found in Taï. Biomass produced in one year was less than that produced in Taï in 5 months (Uhl & Murphy 1981). This might be due to the fact the soils are even poorer in the Amazonian basin. Farmers in those studies subsist mainly on cassava. Unlike shifting cultivators who grow cereals (rice, maize), farmers planting tubers are obliged to clean the forest soil more thoroughly which means extra burning, some tillage to bury the plant material and extra weeding because of the longer growing seasons of cassava and yams (Budelman & Zander 1990, Grenand & Haxiare 1977, Hames & Vickers 1983). In the Taï region both yam farming (by immigrants) and rice cropping (by forest people) occurs. In the fields of the former far fewer resprouting plants occur.

The literature reports (Stocker 1981, Whitmore 1982 and others) that fire and repeated weeding kills off most of the sprouting stems and roots. We conclude that many plants indeed die as a result of this. However, viewing the stabilization of plant densities 3–4 years after felling of the forest, some plants, especially climbers, are capable of site tenure and even expand despite repeated slashing and burning.

Seed bank studies in Taï (De Rouw & Van Oers 1988) have demonstrated that the first colonizers of a new field are largely drawn from the pool of plants already present at the time of cutting, either as established plants or dormant as buried seeds. Studies of young secondary vegetation in Taï showed that these first colonizers will constitute the forest fallow if a field is abandoned after one rice crop and little weeding is done (Alexandre *et al.* 1978, De Rouw 1991). A rapid process of reforestation is assured by woody pioneers that germinate rather synchronously from seeds surviving in the soil and by outgrowth of shoots. The same type of immediate forest recovery has been documented from fields of upland rice shifting cultivators (Kochummen 1966, Kunkel 1966, Symington 1933) and from sites that have been cut and burnt but not farmed in areas where roots or tubers are the staple crops (Miles 1987, Uhl 1987, Uhl & Murphy 1981, Young *et al.* 1987). In these cases sprouting plants mainly contribute to floristic diversity and do not play an important role in structural forest recovery compared with pioneer trees grown from seed. The competitive advantage of plants already growing on the site or present in the seed bank, over immigrant individuals is reduced by repeated slashing and burning. It destroys the seed stock, weakens resprouting plants and creates open spaces filled by species that have a very effective means of dispersal, annual weeds and forbs. These plants will re-seed the field almost continuously from that moment on, only checked by weeding or by the installation of a canopy. The same process, destruction of the viable diaspores in the soil resulting in the replacement of the forest fallow by a thicket, has been described elsewhere (Ahn 1958, Smitinand *et al.* 1978, Uhl 1987, Zwetsloot 1981). The rate of succession back to forest in these disturbed fields depends on the ability of coppice shoots to grow in competition with weeds, forbs, grasses, and to occupy the forb canopy and so eventually, drive out the weeds. This ability of sprouting plants to exclude and suppress weeds has been used in some shifting cultivation systems suffering from land shortage (Vine 1954). Deliberate preservation of stumps in shifting cultivation systems was also mentioned by Delvaux (1958), Aweto (1981) and by Zinke, *et al.* (1978). One example of this was found in the Taï area, in two flat rather swampy areas (total of 640 ha, De Rouw *et al.* 1990). Upland rice is cropped for one season and fallows are surprisingly short, not exceeding six years. As no primary or old secondary forest is left, the region must have been cropped for rice over a long time. This was confirmed by the study of aerial photographs of 1956 and by interviews with farmers. Many of the weeds present belong to stout, climbing Marantaceae (*Hypselodelphys violacea*, *Marantochloa* spp). These are cut back during the cropping period but at the end of the season are allowed to grow out. Their large leaves and vigorous growth assure a quick ground cover thus preventing the spread of heliophyl weeds, sedges and grasses but not the growth of pioneer trees. One condition is the removal of *Chromolaena odorata* seedlings during the cultivation period.

This thicket-forming weed constitutes the only severe threat to the installation of a fallow vegetation comprising both pioneer trees and Marantaceae climbers.

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