CHAPTER 7

SEEDLINGS, SAPLINGS AND TREE TEMPERAMENTS: POTENTIAL FOR AGROFORESTRY IN THE AFRICAN RAIN FOREST

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INTRODUCTION

Recent results from experimental treefall gaps in tropical forest have demonstrated that gap size has less influence than expected on tree density and floristic composition following gap opening (Uhl et al., 1988; Brown and Whitmore, 1992; Kennedy and Swaine, 1992). Rather than the occurrence of new species from the seed bank, what appears to be the most important change is the rate of vegetative growth of the various trees in place, either as seedlings, or juveniles, or mature individuals. By contrast, after slash and burn cultivation, vegetation changes are a result of both seedlings from the seed bank in soil, and sproutings from individual plants surviving after fire. The balance between these two processes depends on the history of the site, on the previous cultural practices and on the species cultivated (Mitja and Hladik, 1989; see review in de Rouw, 1993).

The germination of tropical tree seeds is generally immediate and their viability is very short (Ng, 1978; Miquel, 1987). Seed dormancy is a characteristic of few tropical species (Vázquez-Yanes and Orozco-Segovia, 1990). However, tree seedlings and saplings of many species can survive in the undergrowth of a tropical forest for several years and wait for favourable light conditions to start growing (Hallé et al., 1978; Whitmore, 1990).

In this context, the adaptive strategies of seedlings of trees and lianas of the Gabon rain forest were related to seedling morphology (Miquel, 1987). The resulting plant establishment in plots was analysed in terms of proportions of the various seedling types from which trees and lianas originated (Hladik and Miquel, 1990). The success of sapling establishment (Hladik and Blanc, 1987) as well as lifetime performances of tree species were studied by measuring survival and growth rates in permanent plots (Hladik, 1982).

All biological and ecological characteristics of forest species, which define a species' temperament (*sensu* Oldeman and van Dijk, 1991), are essential for understanding forest dynamics. Data presented here may provide useful information for future tropical agroforestry systems.

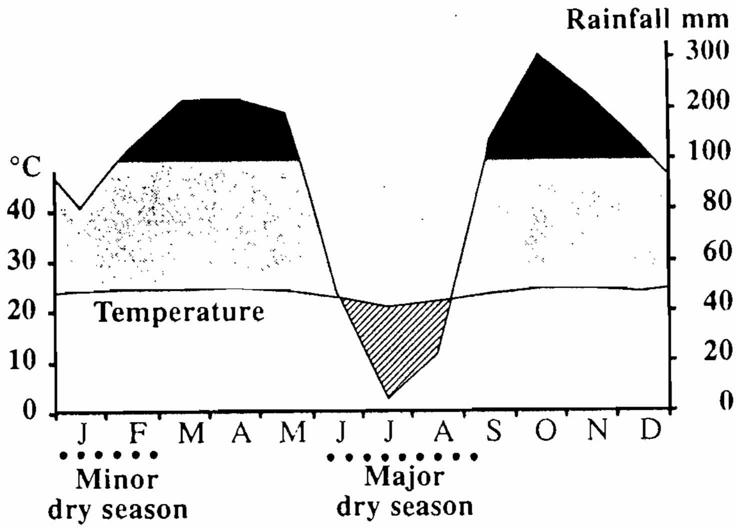

Figure 7.1 Climatic diagram of the Makokou area (Gabon), showing mean monthly temperatures (1953–1975) and mean monthly rainfall (1951–1975)

THE STUDY AREA

The station where the observations of seedlings and saplings were carried out is located in Gabon, near Makokou (0° 31′ North 12° 48′ East, at about 500 m altitude), inside the biosphere reserve of UNESCO. This permanent field station allows long-term studies to be sustained in the African rain forest, and data have been collected in this area since the early 1960s (Anon., 1987).

The Makokou forest has an annual rainfall of 1,700 mm and a mean temperature of 24 °C. The major dry season (Figure 7.1), is accompanied by low temperatures because of a persistent cloud cover allowing a wet evergreen forest to be maintained in spite of limited annual rainfall. Some deciduous tree species are present in Makokou (Hladik, 1978); but there is no species such as *Triplochiton scleroxylon* (Sterculiaceae), *Ceiba pentandra* (Bombacaceae), or *Terminalia* spp. (Combretaceae) characterizing semi-deciduous forests. Tree species diversity is lower than that of Asia, but is as high as that of most American rain forests (e.g. forty to fifty species per hectare for trees over 30 cm diameter, Hladik, 1986), including several leguminous tree species, especially Caesalpiniaceae (35 per cent of the total basal area).

Two five-year-old fallows where the observations of plant regrowth were carried out are also located near Makokou, but outside the biosphere reserve. In this area, shifting cultivation is practised after burning forest plots or old fallows of about a quarter of one hectare per family. Mixed fields of manioc, including plantains, yams and maize, are used for two or three years without weeding. Since population density is low, the period of fallow may last for more than twenty years, during which tree species participate in vegetation recovery.

SEEDLING TYPES AND SEED DISPERSAL

Faced with the large number of morphological and functional adaptations of seedlings of the various tropical trees, several authors have proposed a classification according to the role of the cotyledons. Duke (1965) was the first to introduce two contrasting terms for tropical seedlings: phanerocotylar, applied to seedlings with exposed cotyledons; and cryptocotylar, applied to seedlings with cotyledons hidden in the seed coat. Duke discussed the occurrence of these two categories according to environmental conditions, especially light intensity and humidity. The seedling types that were previously described, mostly from observations in temperate zones, referred exclusively to the hypocotyl: epigeal and hypogeal, respectively with a hypocotyl and without (or with a very reduced) hypocotyl. Ng (1978) combined these two classifications, making four seedling types.

After Garwood (1983) had emphasized the important difference between green foliaceous, photosynthetic cotyledons versus fleshy cotyledons, which are rich storage organs, Miquel (1987) recognized – among 210 species in the Makokou forest – the five distinctive seedling types illustrated in Figure 7.2. These five types, adopted in this paper, are defined as follows:

(1) Exposed leafy cotyledons above ground level (epigeal), with photosynthetic capacity and no reserve;
(2) Exposed fleshy cotyledons above ground level (epigeal);
(3) Exposed fleshy cotyledons at ground level (semi-hypogeal);
(4) Cryptic cotyledons at ground level or below ground (hypogeal); and
(5) Cryptic cotyledons above ground level (epigeal).

A comparison of various tropical forests, using this seedling classification, revealed that the frequencies of the five types are very similar on different continents (Miquel, 1987; Hladik and Miquel, 1990). The most abundant seedling type among the tropical rain forest species is the first one – with foliaceous photosynthetic cotyledons – accounting for about 40 per cent of the species (whereas, in the temperate zone, this type occurs in 95 per cent). Seedling type 2 (25 per cent) and seedling type 4 (22 per cent) are also abundant. Seedling type 3 is less frequent (9 per cent), but the rarest (5 per cent), is type 5. Although described as 'suicidal', because the plants die when the cotyledons remain locked inside the seed coat if raised in the dry conditions of a nursery, this last type is present in all tropical forests. It is quite successful, since most species of this type are abundant.

In the heterogeneous structure of a rain forest, each of these five seedling types have to live with various potentially limiting factors – light intensity,

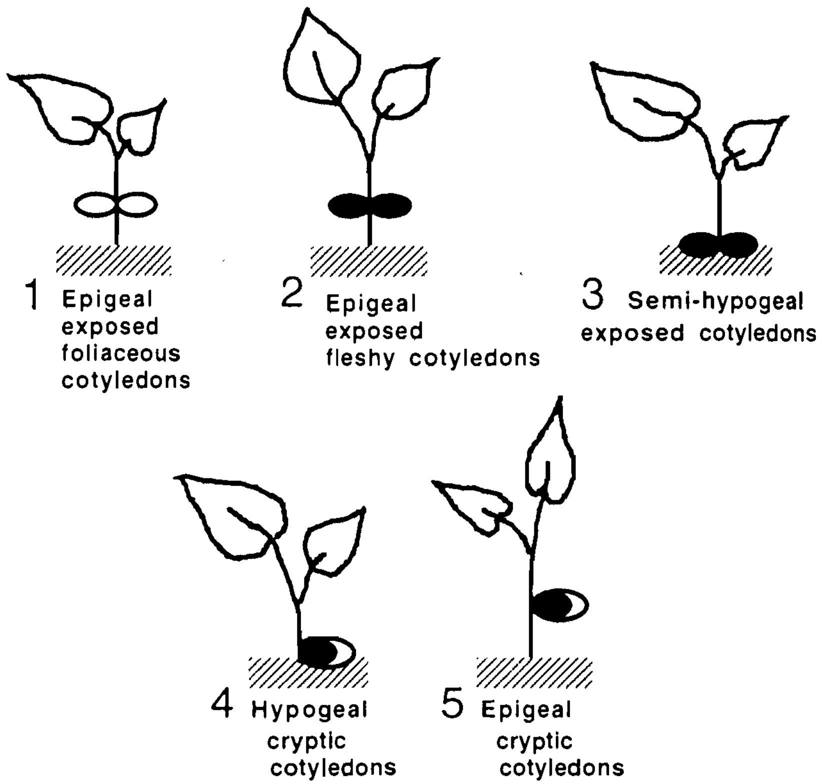

Figure 7.2 The five distinctive seedling types of tropical species, based on hypocotyl and cotyledon morphology (source: Miquel, 1987)

light spectral composition, carbon dioxide level, temperature and humidity – according to their photosynthetic capacity, potential resting stages with storage organs, and the resulting growth rate for above and below ground parts. However, it might be difficult to distinguish the limit between type 1, with green photosynthetic foliaceous cotyledons, and type 2 with fleshy storage cotyledons which are sometimes green. The study of Kitajima (1992), based on measurements of the thickness and photosynthetic efficiency of cotyledons of ten species from Barro Colorado Island (Panama), demonstrated that there is a continuum between these two types.

The spatial distribution of different seedling types mostly depends on the behaviour of animal populations, since many tropical plants bear fruits with the 'animal syndrome' of seed dispersal. These relationships have been generally studied according to the fruit and seed type and to the specific animal characteristics – body weight, oral cavity and digestive tract, home range activity in time and space – (see review in Estrada and Fleming, 1986; Fleming and Estrada, 1993). The seedling type, which is particularly important for the success of plant establishment, was more recently taken into consideration in seed dispersal systems (Hladik and Miquel, 1990).

Seed size is the first parameter to be considered in relation to animal dispersal and seedling establishment. All seedlings from small seeds (below 5 mm as measured along the largest axis, excluding wing) have the foliaceous cotyledons of seedling type 1. Species with seeds of medium and large size may have seedlings of any of the five types. For instance, very large leaf-like cotyledons can emerge from large seeds of the forest species such as *Picralima nitida* (Apocynaceae), *Panda oleosa* (Pandaceae), and many species of the Sapotaceae family. However, there is no seedling type 5 among species with very large seeds, and one can wonder whether these seeds are too heavy to be supported by a hypocotyl.

Among plant species actually dispersed by vertebrates in the Makokou rain forest (Gautier-Hion et al., 1985), those with seedling type 1 are dispersed by the largest array of animals: the elephant, six primate species, seven large birds, seven ruminants, nine squirrels, eight small rodents and two large rodents. Seeds from these plant species take advantage of being dispersed over long distances, thus increasing their chance to reach a place with enough light in the forest mosaic for the immediate photosynthetic requirements.

As shown in Figure 7.3, species with seedling types 2 to 5 are dispersed by a more limited number of animals than those with seedling type 1. There are few species with seedling type 3 (only 9 per cent out of the 210 species studied at Makokou) and they are rarely dispersed by animals, being mostly autochorous (with fruits falling directly on the ground). Some seedling types, within specific seed size categories, are dispersed by particular animals; for instance, dispersal of plants with seedling type 4 (e.g. liana species of the Apocynaceae and Dichapetalaceae families) depends on monkeys, whereas plants with seedling types 1 and 2, with the largest seeds, depend exclusively on the elephant.

SAPLING GROWTH AND FOREST DYNAMICS

Established seedlings, after about 1 year, are usually called saplings. Sapling growth has been monitored on permanent plots in the Makokou rain forest during a 64-month study (about 5 years). Plant survival and growth rate were measured on two 50 m transects, one in undisturbed forest and the other in a recent single treefall gap (Hladik and Blanc, 1987). These data are discussed here in relation to seedling types.

The two transects were selected to show the effect of light availability on the growth of different species. Cumulative total incident light has been measured in 1980 and 1985, and expressed as the relative incident light. These measurements were made in ten locations and include the variation between days as well as

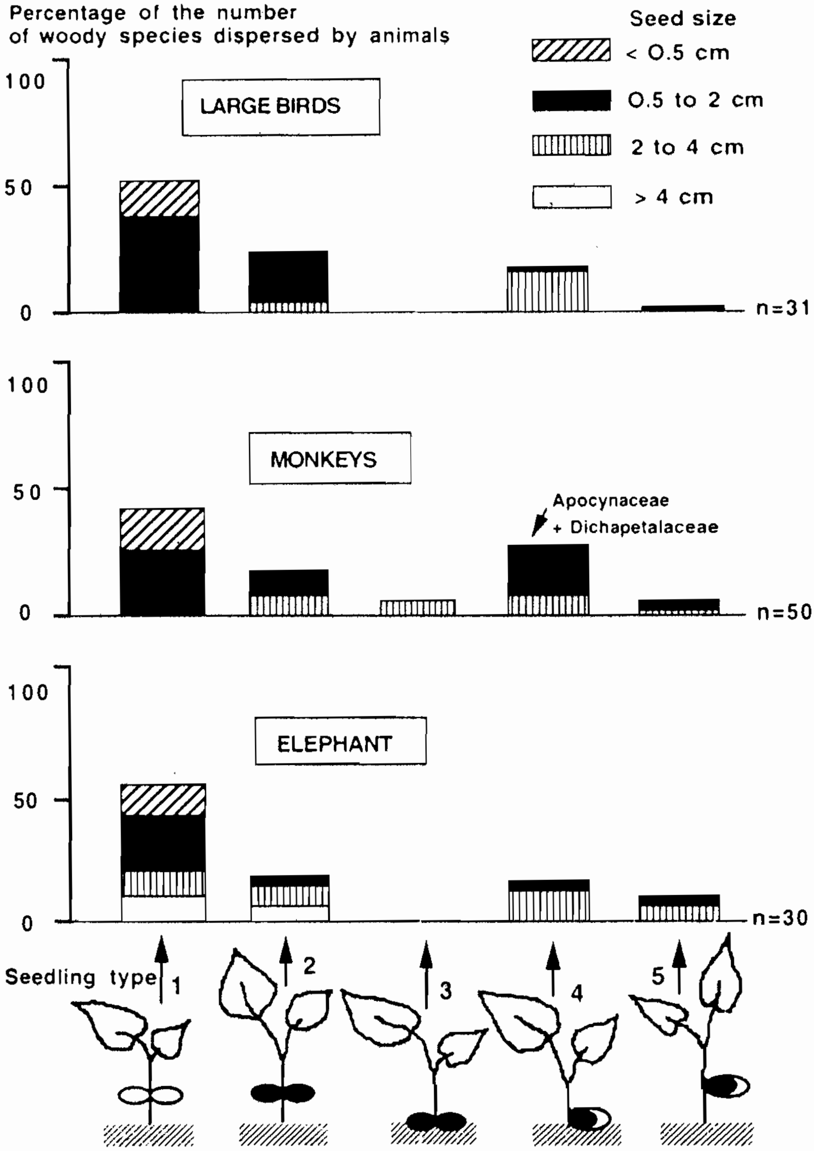

Figure 7.3 Percentage of woody species with different seedling types dispersed by three major animal groups of the Makokou forest, in relation to seed size (source: Hladik and Miquel, 1990)

diurnal sunfleck variation. As far-red and infra-red were included in the total light measurement, the minimum observed in one site was 2 per cent of incident light, whereas 1 per cent is the mean value generally obtained with a standard quantum sensor in the undergrowth of a rain forest. The mean relative light intensity varied from 8.5 to 3.4 per cent in the tree gap and from 3.0 per cent to 4.3 per cent in the undisturbed forest between 1980 and 1985, as a result of the changes in the forest structure: a progressive closing of the treefall gap and a slight opening of the undergrowth, where large branches had fallen.

Plants measuring 20 cm to 3 m tall were marked with aluminium tags in ten plots (4 × 4 m) adjacent to the light measurement sites, including at least fifty shrubs and saplings of trees and lianas. Identification of these 500 plants was made in the field, without taking herbarium samples to avoid trauma to the plants. Accordingly, some individuals that died before July 1982 remained unidentified. Liana species showed the highest rate of mortality: 57 per cent and 72 per cent respectively in the undisturbed forest and in the treefall gap. For tree species, the mortality was respectively 38 per cent and 50 per cent, and for the shrub species, adapted to life in the undergrowth of the forest, 25 per cent and 51 per cent. The lianas showed the highest growth rate in the tree gap (a mean of 141 per cent of the initial size, whereas tree growth was 96 per cent and shrub growth 65 per cent, over the five years). But, at the community level, however, the handicap of a slower rate for the trees is offset by the higher mortality rate of lianas (see details in Hladik and Blanc, 1987).

The percentage height increment of each species of the tree saplings (for surviving saplings) of these two transects (116 individuals) is presented in Table 7.1, in which the forty-four tree species have been grouped according to seedling types. Due to the higher light availability in the treefall gap, the total growth increment of tree saplings is more than double that in the undisturbed forest (103 per cent versus 40 per cent). The only exceptions are species with seedling type 5, because these plants died in the dry conditions of the treefall gap.

Intraspecific comparisons can be made for ten species present in both transects. Among species with seedling type 1, *Heisteria parvifolia* displayed its best performance in the treefall gap, although it survived in the undergrowth.

The best mean growth rate was found among tree species with seedling type 2. This performance was also found in experimental cultivations (see Discussion). One of the most common species of the Makokou forest, *Scorodophloeus zenkeri*, had a similar increment in the undergrowth and in treefall gap. The maximum growth rate (400 per cent) appeared during the first three years of observation, in a young *Milletia mannii*, although this pioneer tree was almost dead in 1985, the tree gap being initially too small and slowly closing.

The general trend that appears in comparing the proportions of species with various seedling types among these observed saplings, with the initial number

Table 7.1 Height increment of tree saplings in undisturbed forest and in a treefall gap within the Makokou forest, over a 5-year period. Species are grouped according to seedling types (source: Hladik and Blanc, 1987 and unpublished data)

	Undisturbed forest			*Treefall gap*		
	Initial number of individuals	*Final number of living trees*	*Percentage height increment of surviving saplings*	*Initial number of individuals*	*Final number of living trees*	*Percentage height increment of surviving saplings*
Species with seedling type 1 						
Heisteria parvifolia	3	3	30	2	1	150
Gambeya boukokoensis	1	1	67	1	1	125
Grewia coriacea	2	0	0	1	0	0
Strombosia grandifolia	2	2	30	0		
Drypetes sp. (AH 4667)	2	2	30	0		
Drypetes sp. (AH 4670)	2	2	25	0		
Baphia pubescens	1	1	34	0		
Drypetes sp. (dead)	1	0	0	0		
Gambeya africana	0			1	1	33
Pausinystalia macroceras	0			1	1	113
Xyopia sp. (dead)	0			1	0	0
Petersianthus macrocarpus (dead)	0			2	0	0
Species with seedling type 2 						
Scorodophloeus zenkeri	4	2	53	7	4	74
Piptadeniastrum africanum	1	1	68	0		
Dialium pachyphyllum	4	4	45	0		
Dacryodes klaineana	3	3	30	0		
Trichilia sp. (AH 4736)	2	2	6	0		
Milletia sp. (AH 4735)	1	1	34	0		
Milletia mannii	0			1	1	400
Dacryodes buttneri	0			1	1	78
Santiria sp. I (AH 2986)	0			1	1	12
Santiria sp. II (AH 2941)	0			2	2	125

Milletia sp. (AH 4735)	1	1	34	0		
Milletia mannii	0			1	1	400
Dacryodes buttneri	0			1	1	78
Santiria sp. I (AH 2986)	0			1	1	12
Santiria sp. II (AH 2941)	0			2	2	125

Trichilia sp. (AH 4709)	0			2	2	123
Trichilia sp. (dead)	0			2	0	0
Species with seedling type 3 						
Pentaclethra eetveldeana	15	5	5	8	2	40
Cola rostrata	1	1	3	1	1	80
Species with seedling type 4 						
Pancovia pedicellaris	3	0	0	4	3	85
Garcinia sp. (AH 4669)	2	2	27	1	1	21
Laccodiscus sp.	1	1	25	0		
Carapa procera	1	1	38	0		
Eriocoelum macrocarpum	0			1	1	180
Pycnanthus angolensis (dead)	0			1	0	0
Staudtia gabonensis (dead)	0			1	0	0
Lophira alata (dead)	0			1	0	0
Parinari excelsa (dead)	0			1	0	0
Beilschmedia sp. (dead)	0			1	0	0
Species with seedling type 5 						
Polyalthia suaveolens	2	2	34	2	0	0
Plagiostyles africana	1	1	70	1	0	0
Coula edulis	2	2	95	0		
Afrostyrax lepidophyllus	7	1	33	0		
Anonidium mannii (dead)	1	0	0	0		
Species with seedling type unknown						
Diospyros piscatoria	1	1	25	0		
Sorindeia nitidula	0			1	1	50
Anacardiaceae (AH 4679)	0			1	1	30
Total	66	41		50	25	
Mean height increment			40			103

of species with seeds dispersed in the same area, is a reduction of type 1 (from 39 per cent to 27 per cent of the observed species), and an increase of type 5 (from 5 to 11 per cent). This trend appears to be accentuated if we consider the present mature forest composition, with only 20 per cent of the tree species (over 5 cm dbh) originated from seedling type 1, and the same proportion from seedling type 5.

TEMPERAMENTS OF TREE SPECIES

In their search for the most accurate description of the growing capacities of tree species, foresters and botanists have proposed several classifications, generally in relation to species' responses to light availability. Swaine and Whitmore (1988) provided a clear definition, based on seed and seedling ecology, of the two qualitatively distinct groups of tree species, respectively known as the 'pioneers' and the 'climax' (or non-pioneer) species. They also follow the concept of a continuum within each of these groups, although the attempted subdivisions previously proposed are arbitrary segments of this continuum. A comparison of the growth patterns of various tree species in the mature phase forest may help clarify these distinctions.

Tree growth, mortality and recruitment in the Makokou forest have been monitored during 7 years (1972–79), on two permanent plots of 4,000 m^2 (400 m × 10 m) and of 9,000 m^2 (1,800 m × 5 m), including respectively 397 trees with dbh > 5 cm belonging to ninety-two species and ninety-three trees with dbh > 30 cm belonging to forty-one species. The overall mortality was 10 per cent compensated by growth and recruitment (see details in Hladik, 1982). The major data concerning pioneer and non-pioneer species are presented in Table 7.2 according to species seedling types.

There are few pioneer trees in the forest mosaic (including treefall gaps, mature phase forest, and all the intermediate phases). In the study plots, which did not include any recent treefall gaps, the first four species in Table 7.2, for which the maximum growth increment during the study period was 48 per cent of the initial basal area, were represented by scarce individuals. Nevertheless, these species, which all have seedling type 1, account for 9 per cent of the total basal area. The next twelve species presented in Table 7.2 account for 50 per cent of the total basal area and reveal various growth patterns. For most of these species, the number of individuals in the forest was sufficient to show significant differences ($p < 0.05$; *t*-test).

Species with seedling type 1 are also included among those abundant species, for instance *Panda oleosa*, a medium-sized tree abundant in the Makokou forest (20 per cent of the total basal area of the plot) only had an increment of 4 per cent of the initial basal area over the 7-year study. In contrast, *Heisteria parvifolia*, a common small tree, may grow fast when enough light is available, as already shown above for its saplings.

Table 7.2 Basal area increment of tree species in undisturbed forests at Makokou, over a 7-year period. Species are grouped according to seedling types (source: Hladik, 1982 and unpublished data)

	Initial number of individuals	*Final number of living trees*	*Recruitment*	*Basal area* (m^2) 1972	*Basal area* (m^2) 1979	*Basal area increment* (%)
Pioneer species						
Species with seedling type 1 						
Macaranga barteri	4	2	0	0.21	0.31	47.0
Ficus macrosperma	1	1	0	0.81	1.21	48.0
Croton oligandrus	1	1	0	0.12	0.26	40.0
Alstonia boonei	3	2	0	0.57	0.64	13.0
Non-pioneer species						
Panda oleosa	18	18	0	8.03	8.35	4.0
Petersianthus macrocarpus	8	7	1	0.83	0.88	6.7
Heisteria parvifolia	13	12	1	0.39	0.47	19.2
Species with seedling type 2 						
Scorodophloeus zenkeri	35	31	4	3.16	3.37	6.5
Santiria sp. II	21	24	4	1.20	1.37	14.5
Species with seedling type 3 						
Pentaclethra eetveldeana	9	9	0	1.78	1.88	5.4
Cola rostrata	8	8	1	0.23	0.27	7.0
Species with seedling type 4 						
Pycnanthus angolensis	1	1	0	0.31	0.46	40.0
Species with seedling type 5 						
Polyalthia suaveolens	27	27	0	0.97	1.08	11.5
Plagiostyles africana	21	20	1	1.05	1.12	6.0
Anonidium mannii	11	11	0	0.56	0.61	9.6
Coula edulis	8	8	1	0.89	1.00	11.5

Species with seedling type 2 also have characteristic growth patterns. For instance, the most common species in the plot, *Scorodophloeus zenkeri*, had a slow growth rate (6.5 per cent), whereas the best performance in this category was for *Santiria* sp. II (14.5 per cent).

Among species with seedling type 3, *Pentaclethra eetveldeana*, which has a high mortality rate among saplings, shows, in mature phase forest, a low growth rate (5.4 per cent), as does *Cola rostrata* (7.0 per cent).

Only one species with seedling type 4, *Pycnanthus angolensis*, is presented in Table 7.2. Although present in the mature phasae of the forest mosaic, this species' high growth rate (40 per cent of the initial basal area) would place it, in the continuum of non-pioneer species, very close to the pioneers.

Species with seedling type 5 are typically shade-tolerant, and thus non-pioneers, but among them, species such as *Polyalthia suaveolens*, and *Coula edulis*, both abundant in the Makokou forest, have increments higher than 11 per cent. In contrast, the increment was only 6 per cent for *Plagiostyles africana*.

These differences in growth potential during the mature phase of various species are thus complementing the adaptations of seedlings and saplings to grow in various environmental conditions. Altogether, these differences, which characterize the species' temperament, are of great significance to population dynamics.

PLANT REGROWTH IN FALLOWS: SEEDLINGS *VERSUS* RESPROUTS

Species' temperaments are particularly obvious after shifting cultivation, when the vegetation is reconstructed in the recent fallows such as those described by Mitja and Hladik (1989). For this study, the demographic composition of the annual herbs and perennial woody plants were determined along narrow transects (1 m wide), including 14,000 plant individuals, and covering a total area of 300 m^2 in two 5-year-old fallows.

The seedlings, saplings and 'adult' plants were counted, the adult stage being defined according to size, but not necessarily corresponding to the reproductive stage. For an approach to population dynamics, since repeated surveys were not feasible, the observed cumulative changes over 5 years of fallow growth were used to forecast future changes.

Four demographic groups, based on relative proportions of seedlings, saplings and adults were defined for the tree species as follows:

(I) Group I: short-lived species, exclusively herbaceous plants and shrubs, with many senescent adults in the plots.

(II) Group II: adult tree species with few seedlings in the plots. Most species of this group have been described as pioneers.

(III) Group III: small, rapidly maturing trees and the seedlings germinated from their seeds.

(IV) Group IV: tree species with no adult and few seedlings in the plots. Trees of this group are known as the long-lived species of the forest.

Data on the tree species (860 individuals belonging to at least thirty-seven species), are presented in Table 7.3, to show the demographic groups (when a sufficient number of individuals was found) in relation to seedling types. Most of these plants (twenty-six species, accounting for 75 per cent of the total number of individuals and for three-quarters of the basal area) originated from the seedling type 1 with foliaceous cotyledons. This high proportion of plants with seedling type 1, much higher than that found inside the forest, is a characteristic of the open areas (Hladik and Miquel, 1990). These twenty-six species are distributed amongst the three demographic groups (II, III, IV). The measurement of the sprouting capacities, together with the demographic analysis, provided additional data about species' temperament.

Among species belonging to demographic group II, *Musanga cecropioides*, *Trema guineensis*, *Harungana madagascariensis* and *Pauridiantha callicarpoides* regenerated from seedlings. Others species such as *Macaranga monandra* and *Rauvolfia vomitoria*, regenerated partly from seedlings and partly from sprouting (20–30 per cent). Moreover, some species, such as *Caloncoba welwitschii*, regenerated exclusively by sprouting.

Sprouting capacity is not limited to tree species with the seedling type 1. *Myrianthus arboreus*, with seedling type 4, and *Albizia adianthifolia* with seedling type 2, also regenerate by sprouting. This capacity, revealed after severe treatment such as trunk cutting or fire, can be rarely observed within the rain forest. Several species of the genus *Albizia* that grow at the interface between forest and savannah, are well known to be fire-resistant.

Human activities such as frequent clearing, cutting and burning encourage some particular species to dominate either by sprouting or from seedlings. These species are generally described as pioneer although the definition related to seed and seedling ecology (Swaine and Whitmore, 1988), does not apply to all of them.

The degree of species dominance in regrowth vegetation, either from resprouts, or from seedlings, reflects the cultural process to which the cultivated plot was submitted (Mitja and Hladik, 1989). For example in Gabon, after the initial forest clearing, *Musanga cecropioides* dominates in fallows, whereas in the area submitted to a limited number of successive cycles of cultivation, *Trema guineensis* dominates; both species regenerate from seedlings. In contrast, in areas where shifting cultivation has been practised for many years (with many successive field–fallow cycles), *Trema guineensis* tends to decrease in density and the number of individuals of the species which can resprout increases.

Table 7.3 Comparison of the numbers of seedlings, saplings and 'adults' in the populations of trees species in five-year-old fallows of the Makokou area. The resulting demographic groups (see text) and the sprouting capacities are presented in relation to species' seedling types (source: Mitja and Hladik, 1989 and unpublished data)

	Basal area (cm^2) for trees > 2 m	*Number of seedlings*	*Number of saplings*	*Number of 'adults'*	*Total number of individuals*	*Demographic group*	*Percentage of sprouting for trees > 2 m*
Species with seedling type 1							
Trema guineesis	523	0	25	16	41	II	0
Harungana madagascariensis	134	0	0	11	11	II	0
Pauridiantha callicarpioides	69	0	18	4	22	II	0
Musanga cecropioides	58	10	0	1	11	II	0
Macaranga monandra	49	0	7	1	8	II	20 (5)
Rauvolfia vomitoria	29	0	14	14	28	II	25 (8)
Psidium guajava	41	1	4	10	15	II	0
Macaranga spinosa	42	3	10	8	21	II	0
Ficus exasperata	10	3	15	3	21	II	0
Caloncoba welwitchii	7	0	7	6	13	II	100 (3)
Leea guineesis	3	45	54	17	116	III	
Vernonia cf. conferta	53	165	5	7	177	III	
Ficus sur	42	0	0	1	1		33 (2)
Anthocleista schweinfurthii	—	0	1	3	4		
Sapium cornutum	—	0	1	1	2		
Distemonanthus benthamianus	62	9	30	0	39	IV	80 (5)
Petersianthus macrocarpus	31	1	7	0	8	IV	50 (4)
Markhamia sessilis	9	1	14	0	15	IV	0

Bridelia atroviridis	8	26	37	0	63	IV	0
Bridelia cf. micrantha	—	1	16	0	17	IV	0
Fagara sp.	26	0	2	1	3		
Tricalysia sp.	18	0	1	1	2		
Gambeya boukokoensis	4	0	0	2	2		
Duboscia macrocarpa	—	0	0	2	2		
Xylopia hypolampra	—	0	1	0	1		
Lindacheria dentata	—	0	1	0	1		
Species with seedling type 2 							
Milletia mannii	195	87	63	18	168	III	0
Albizia adianthifolia	122	1	1	8	10	II	100 (8)
Piptadeniastrum africanum	—	1	2	0	3		
Dialium sp.	—	0	1	0	1		
Species with seedling type 3 							
Pentaclethra eetveldeana	133	0	1	11	12	IV	75 (11)
Pterocarpus soyauxii	—	0	1	0	1		
Species with seedling type 4 							
Myrianthus arboreus	88	2	1	5	8	II	100 (4)
Anthonotha macrophylla	13	0	0	4	4		
Pycnanthus angolensis	23	0	0	1	1		
Species with seedling type 5 							
Anonidium mannii	—	0	6	1	7		
Plagiostyles africana	—	0	1	0	1		
Species with seedling type unknown (three species)							
	35	0	5	6	11		
Total	1808	356	347	157	860		

DISCUSSION: WHAT ARE THE BEST SEEDLING TYPES AND SAPLING RESPONSES FOR AGROFORESTRY SYSTEMS?

The different species can be characterized by the growth potential of seedlings, saplings and adults, although individual plant behaviour varies during these different phases (Oldeman, 1990). These aspects of species temperament were observed in forest populations where dispersal and seedling establishment are key phases in species' population dynamics, as was emphasized by Schupp et al. (1989) in terms of arrival and survival.

The data presented in this paper focus on the gradual change of sapling and young tree populations. In the artificial environments of fallows, home gardens or agroforestry systems, the growing capacity of these species can be utilized. The introduction of agroforestry systems in Africa, which might partly replicate the efficient systems developed in Asia (Hladik and Hladik, 1984; Foresta and Michon, 1993), necessitates a thorough knowledge of seedling type responses and growth pattern changes throughout the life-cycle of a large number of potentially useful tree species. Since the link between seedling type and tree temperament is evident only for species with seedling type 1, it is important to know both characters for managing tree species.

Most observations about responses of trees introduced in African man-made forests concern species easy to handle in the nursery. They can grow rapidly in the open, and thus have seedling type 1, such as *Trema guineensis*, (Scheepers et al., 1968), *Terminalia* spp., *Aucoumea klaineana*, and most recently tested, *Nauclea diderrichii* (Maldague et al., 1986). In the agroforestry experiments conducted in the Makokou area (Miquel and Hladik, 1984) we tested species with various seedling types, selected for multi-purpose production, particularly fruit production, as well as timber and firewood. Species with seedling types 2 and 3 were efficient in terms of survival and growth. They could be planted either in association with other species, or directly inside fallows and home gardens.

Some examples (Figure 7.4) illustrate this discussion. Among the fruit trees with seedling type 2, *Dacryodes edulis*, the African plum tree (Figure 7.4A), and *Irvingia gabonensis*, the 'wild mango tree' (Figure 7.4C) can rapidly reach the height of surrounding plants, most of these having seedlings of type 1. The leguminous tree with seedling type 3, *Pentaclethra macrophylla*, (Figure 7.4B) performed even better than the 'plum tree' after 18 months, probably in response to mycorrhizal association. Among the few species with seedling type 4, *Lophira alata* (Figure 7.4D) can grow rapidly in open places like all other pioneers.

Accordingly, the best choice for agroforestry is not necessarily one species selected for its high performance. As emphasized by Huston (1979), competition is low in a complex environment and the 'best player' when light availability is maximum cannot necessarily express its full potential in an agroforestry system. By grouping plants according to potential growth, an

Figure 7.4 Saplings and young trees with seedling types typical of rain forest undergrowth, raised in experimental fields in the Makokou area. A, 18-month-old *Dacryodes edulis*, the African plum tree (seedling type 2); B, 18-month-old *Pentaclethra macrophylla*, a leguminous tree (seedling type 3); C, 4-year-old *Irvingia gabonensis*, the 'wild mango tree' (seedling type 2); and D, 4-year-old *Lophira alata*, known as a 'pioneer' of large stature (seedling type 4)

agroforestry system, even though it cannot be as complex as a rain forest, may allow efficient development of several tree species for the benefit of mankind.

ACKNOWLEDGEMENTS

We are indebted to the Gabonese government, which made possible the work of scientists at the Makokou Field Station, and to the Smithsonian Institution, which permitted us to start botanical studies in 1971 (postdoctoral fellowship awarded to A. Hladik). Funds available from the CNRS during several years and an additional grant from the MAB Programme of UNESCO supported our long-term studies. We both are grateful to M. Hadley and to M. Swaine for editing our manuscript. We would like to also thank all our colleagues working at the Makokou Field Station, especially H. Cooper who initiated the light measurements; S. Miquel who did a tremendous job on the seedlings survey; P. Blanc who permitted a better understanding of sapling growth; and C.M. Hladik for his help throughout our research work.

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Revised manuscript received September 1994

Hladik A., Mitja Danielle. (1996)

Seedlings, saplings and tree temperaments : potential for agroforestry in the African rain forest

Paris (FRA) ; Carnforth : Unesco ; Parthenon, (17), 173-192. (Man and the Biosphere Series ; 17). ISBN 92-3-103299-2