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Understory vegetation in fast-growing tree plantations on savanna soils in Congo

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Abstract

The hypothesis that tree plantations may catalyze the regeneration of natural forest biodiversity was tested through studies of floristic diversity and structure in fast-growing tree plantations in the Congo. Study sites included experimental and industrial plantations on poor sandy coastal soils near Pointe-Noire, and experimental plantations on clay soils near Loudima. The effects of plantations species, plantation age (in 6- to 20-year-old eucalypt stands), disturbance due to herbicide use and fire, proximity to natural forest, and soils on understory plant diversity were studied. These plantations were compared to the native savanna ecosystem and to adjacent natural secondary forest stands. Vegetation diversity was assessed through analyses of floristic composition, species richness and frequency. Forest species were dominant in the understory of most plantations, especially in the older stands. However, the forest species established in plantation understories were quite different from those from adjacent natural forest stands. *Premna lucens*, *Psorospermum tenuifolium* and *Psychotria* cf. *peduncularis* were the most important forest species found in most eucalypt plantations and in *Pinus caribaea* and *Acacia auriculiformis* plantations. *Alchornea cordifolia*, *Anthocleista nobilis*, *Barteria nigritiana* and *Bertiera* cf. *batesii* were also important. The savanna species *Eriosema erici-rosenii*, *Annona arenaria* and *Loudetia arundinacea* were encountered in many plots. Herbaceous species were dominant in the younger and disturbed plantation stands. © 1997 Elsevier Science B.V.

Keywords: *Acacia*; *Eucalyptus*; Floristic composition; *Pinus*; Regeneration; Species richness

1. Introduction

With increasing areas of eucalypt plantations being established throughout the world, the '*Eucalyptus* controversy' has become an important issue in the tropics (International Foundation for Science, 1989; Calder et al., 1992). The environmental arguments put forward by critics of *Eucalyptus* plantation development in many countries generally focus on their alleged negative ecological impacts, i.e., adverse effects on soil fertility and stability, local hydrology, and wildlife populations. Up to now, most plantation research has dealt with development and productivity of the tree crop, and its site relations and water use. To date, only a limited number of studies have examined the dynamics of plantation understory communities.

Some recent studies have shown that forest plantations can have a 'catalytic effect' on the regeneration of natural forest biodiversity and can be used as a management tool for restoration of degraded lands (Parrotta, 1993, 1995; da Silva Junior et al., 1995). To date, few studies exist on understory vegetation of eucalypt plantations in the Congo (Nongamani, 1988; Sita, 1989; Soler, 1994), or elsewhere in the tropics (e.g., Basanta et al., 1989; Madeira et al., 1989; Lugo et al., 1990; Parrotta, 1995; da Silva Junior et al., 1995; Michelsen et al., 1996), whereas some aspects of understory vegetation of natural euca-

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lypt forest have been studied (Ashton, 1975; Grove, 1988; Ramachandra Swamy, 1992; Bowman and Panton, 1993).

In Congo, eucalypts and other introduced species have been used for experimental and industrial (pulpwood) plantations, mainly on coastal sandy soils in the Pointe-Noire region. Experimental plantations also exist on clay soils in the Loudima region, and on sandy soils in the Brazzaville region. The use of savanna ecosystems in these regions is generally confined to fuelwood collection; commercial and subsistence agriculture by local populations is limited.

The aim of our study is to test the hypothesis that tree plantations may catalyze regeneration of natural forest biodiversity in the Congolese plantations. Biodiversity in understory vegetation was investigated for three fast-growing species, *Pinus caribaea*, *Acacia auriculiformis*, and *Eucalyptus* species, mainly the hybrid *E. alba* x *E. urophylla*, called EPF1 in this area. Impacts of the following variables on biodiversity were studied: age effect in 6-, 10-, 12-, 16-, 18-, and 20-year-old eucalypt stands, disturbance due to herbicide use and fire, stand density, proximity to natural forest, planted species, and soil type. Composition of understory vegetation in the plantations was compared to that of savanna and adjacent natural secondary forest, which is considered to be the final stage in natural vegetation development.

2. Study sites and methods

2.1. Site characteristics

The study areas are located at Pointe-Noire (4° 48′ S, 11° 54′ E) and Loudima (4° 07′ S, 13° 51′ E). The climate is sub-equatorial with a 4-month dry season from June to September. Mean annual precipitation is 1250 mm at Pointe-Noire, and 1070 mm at Loudima. Soils are classified as highly desaturated ferralitic soils in the French classification. Pointe-Noire soils are sandy with >80% sand, whereas Loudima soils are clayey, with >50% clay. Further details on site characteristics were presented previously (Loumeto, 1986; Nongamani, 1988; Bernhard-Reversat, 1993, 1996).

The natural vegetation of plantation sites at Pointe-Noire is grassland savanna, which is generally burnt during dry season. Dominant grasses are *Rhynchelytrum repens*, *Ctenium newtonii* and *Andropogon schirensis*. *Loudetia arundinacea* and *Elionurus argenteus* are frequently locally present in large patches. Several types of forest communities occur. In the valleys, forests are dominated by the tree *Symphonia globulifera*. Coastal thickets have a fringe of pure stands of *Manilkara lacera*. Mangroves also exist in this area (Makany, 1963; Sita, 1989; Dowsett-Lemaire, 1991). At Loudima, native vegetation is a shrub savanna, dominated by the grass *Hyparrhenia diplandra* with scattered shrubs, either *Annona arenaria* or *Bridelia ferruginea* (Koechlin, 1961).

The oldest plantation trials and experimental stands used in this study were established in 1953 by C.T.F.T.,[1] who developed improved methods for planting cuttings of eucalypts (Delwaulle et al., 1981). Cuttings were planted after tilling to a depth of 20 cm, and weeding was done until the second or the third year after planting (Loumeto, 1986; Delwaulle and Laplace, 1988). Industrial plantations have been established since 1978 by U.A.I.C.[2] using similar methods. *Pinus* and *Acacia* plantations were established from tree seedlings raised in the nursery.

2.2. Methods

The following stands were selected for study: 15 *Eucalyptus* stands (hybrid *E. alba* × *E. urophylla*, EPF1), one *Pinus caribaea* stand and one *Acacia auriculiformis* stand on sandy soils in the Pointe-Noire region; one *Eucalyptus* species stand, one *Pinus caribaea* stand and one *Acacia auriculiformis* stand on clayey soils in the Loudima region; the savanna ecosystem at both the Pointe-Noire and Loudima study sites; and native secondary forest at the Pointe-Noire study area. The eucalypt stands in the Pointe-Noire study area included stands representing a range of ages (6, 10, 12, 16, 18 and 20 years), two fire disturbances regimes, two herbicide trials and a control plot without recent herbicide application or fire occurrence. In order to minimize the effects of topography and rainfall distribution on the results, the studied stands were selected on plateau sites, and within a restricted area. However, plots for studies of forest

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[2] Unité d'Afforestation Industrielle du Congo.

proximity and plantation disturbances and an undisturbed control were lacking on plateau sites. These plots were therefore located on gentle slopes. Some of the older plantations used were often disturbed by local people, who occasionally harvest wood for firewood, charcoal-making, poles and construction wood. In these stands, sample plots were chosen in undisturbed areas. Characteristics of the study areas (stands) are given in Table 1.

Vegetation assessments within the stands were conducted using a standard sample plot size of 78.5 m^2 (5-m radius circular plots). The number of plots sampled varied from four to eleven per stand depending on undergrowth density (Table 1). All sample plots were located at least 15 m from plantation edge, within vegetation-rich areas, in order to record the most species for biodiversity assessment. This approach, therefore, yielded in maximum values for plant density, and not average stand values. All woody plants were identified and counted; height and stem diameters were recorded for each individual. Ground cover of herbaceous plants and lianas was recorded using the Braun-Blanquet (1964) cover-abundance scale. Crown density was estimated qualitatively as the amount of shading, i.e. as light, medium or dense. Litter depth for each plot was recorded as the mean of 10 random measurements per plot.

Each species censused was categorized by its natural habitats, or the typical situation in which the species is usually found, based on our knowledge of the vegetation of the region. Four categories were recognized: savanna, forest, planted, and ruderals or gener-

Table 1
Characteristics of stands studied in the Pointe-Noire and Loudima sites

Stand	Plot name	Age (years)	Plantation spacing (m)	No. of plots sampled	Sample area (m^2)	Plantation type	Notes
Pointe Noire							
Savanna	PN Sv	–	–	10	785	–	
Eucalyptus	PN E6	6	5.0 × 3.0	11	863.5	Experimental	1
Eucalyptus	PN E10	10	5.0 × 3.0	10	785	Experimental	1
Eucalyptus	PN E12	12	5.0 × 3.0	8	628	Experimental	1
Eucalyptus	PN E16	16	4.0 × 4.0	8	628	Experimental	1
Eucalyptus	PN E18	18	3.5 × 3.5	7	549.5	Experimental	1
Eucalyptus	PN E20	20	3.5 × 3.5	7	549.5	Experimental	1
Eucalyptus	PN Ef	14	2.5–3.1 × 2.5	4	314	Experimental	2
Eucalyptus	PN EG	14	4.8–6.0 × 6.0	5	392.5	Experimental	2
Eucalyptus	PN Cont	11	4.7 × 3.0	9	706.5	Industrial	3
Eucalyptus	PN H1	11	4.7 × 3.0	7	549.5	Industrial	4
Eucalyptus	PN H2	11	4.7 × 3.0	7	549.5	Industrial	4
Eucalyptus	PN F1	11	4.7 × 3.0	8	628	Industrial	5
Eucalyptus	PN F2	12	4.7 × 3.0	8	628	Industrial	5
Eucalyptus	PN LS1	12	5.0 × 3.0	6	471	Industrial	6
Eucalyptus	PN LS2	12	5.0 × 3.0	7	549.5	Industrial	6
Pinus	PN Pc	15	3.5 × 3.5	8	628	Experimental	
Acacia	PN Aa	12	3.5 × 3.5	5	392.5	Experimental	
Natural forest	PN For	–	–	6	471	–	
Loudima							
Savanna	LDM Sv	–	–	7	549.5	–	
Eucalyptus	LDM Eu	26	2.5 × 2.5	6	471	Experimental	
Pinus	LDM Pc	26	2.5 × 2.5	6	471	Experimental	
Acacia	LDM Aa	11	3.5 × 3.5	6	471	Experimental	

Notes: Stands used to evaluate: [1]effect of plantation age; [2]effect of plantation spacing; [3]control plot for herbicide and fire effects (plot undisturbed by fire or herbicide since July 1993); [4]effect of herbicide (Round-Up) application in April 1994 for PN H1 and January 1995 for PN H2; [5]effect of fire, October 1990 and November 1993 for PN F1, November 1993 for PN F2; [6]effect of distance from forest edge, 10 m for PN LS1 and 50–100 m for PN LS2.

Table 2
Mean values for stand variables for the stands sampled in the Pointe-Noire and Loudima study areas

Stand	Plot	DBH (cm)[a]	Height (m)[a]	Basal area (m^2/ha)	Density (trees/ 100 m^2)	Litter depth (cm)	Crown density	Ground cover[b]	
								Woody	Herb
Pointe Noire									
Savanna	PN Sv	–	–	–	–	0	None	2	5
Eucalyptus	PN E6	16.2 (0.10)	23.8 (0.16)	13	6.2	2.8	Light	1	2
Eucalyptus	PN E10	16.7 (0.19)	24.6 (0.29)	12.8	5.7	3.6	Light	2	1
Eucalyptus	PN E12	18.1 (0.17)	28.9 (0.06)	13.7	5.3	4.1	Light	3	1
Eucalyptus	PN E16	15.9 (0.13)	23.6 (0.26)	15.8	7.8	2.2	Light	4	1
Eucalyptus	PN E18	14.4 (0.26)	23.9 (0.32)	9.4	5.5	4.5	Light	4	2
Eucalyptus	PN E20	18.4 (0.10)	28.2 (0.18)	20.2	7.2	3.8	Light	5	+
Eucalyptus	PN Ef	13.5 (0.16)	23.4 (0.22)	16.1	10.8	2.2	Light	3	3
Eucalyptus	PN EG	17.0 (0.23)	26.8 (0.26)	8.9	3.8	2.6	Light	2	2
Eucalyptus	PN Cont	13.0 (0.03)	19.9 (0.16)	11.3	8.4	3.1	Light	3	4
Eucalyptus	PN H1	12.7 (0.10)	22.2 (0.16)	9.6	7.5	5	Light	3	3
Eucalyptus	PN H2	13.7 (0.13)	21.6 (0.20)	14.6	9.6	4.9	Light	2	3
Eucalyptus	PN F1	13.0 (0.14)	18.9 (0.16)	10	7.5	1.6	Light	2	4
Eucalyptus	PN F2	13.7 (0.18)	21.4 (0.25)	8.5	5.6	3.3	Light	3	4
Eucalyptus	PN LS1	15.4 (0.11)	23.5 (0.12)	15.4	8.2	3.7	Light	3	2
Eucalyptus	PN LS2	14.8 (0.12)	21.9 (0.18)	11.8	6.7	2.7	Light	3	2
Pinus	PN Pc	22.7 (0.29)	22.1 (0.18)	31.5	7.5	6.7	Dense	3	2
Acacia	PN Aa	13.4 (0.27)	14.3 (0.33)	14.1	9.3	3.9	Medium	5	1
Natural forest	PN For	–	–	–	–	1.3	Dense	5	+
Loudima									
Savanna	LDM Sv	–	–	–	–	0	None	2	5
Eucalyptus	LDM Eu	15.5 (0.21)	25.1 (0.25)	28.5	14	2.1	Light	4	2
Pinus	LDM Pc	24.0 (0.31)	26.1 (0.23)	48.5	10.2	2.7	Dense	4	2
Acacia	LDM Aa	12.8 (0.25)	16.4 (0.29)	10	7.2	2.2	Medium	5	1

[a]DBH and height are expressed as means with standard errors in parentheses.
[b]Woody and herbaceous ground cover values according to the Braun–Blanquet scale.

alists. 'Savanna species' are found in the grassland and shrub savannas in which the plantations were established. 'Forest species' are found in the native forest, in secondary forest edges or in forest gaps. 'Planted species' include the planted timber species which form the stands, or which were planted in the neighborhood. 'Ruderal species' are commonly found in disturbed vegetation (roadsides, early stages in fallows, burnt sites, etc.). The herbaria of ORSTOM Centre at Pointe-Noire and C.E.R.V.[3] at Brazzaville, in the Congo, were used for the botanical identification of samples.

Species frequencies were calculated as the proportion of plots in which each species was found. Correspondence analysis was used to determine the relationships between the stands and the species, based on the species lists for each stand.

[3] Centre d'Études des Ressources Végétales

3. Results

3.1. Stand characteristics

The characteristics of the studied stands are summarized in Table 2. Variation in the mean DBH and height among the sampled stands was low. The height range was 19 to 29 m in the *Eucalyptus* stands, 22 to 26 m in the *Pinus* stands, and 14 to 16 m in the *Acacia* stands. Stand density ranged from 530 to 960 stems/ha in the *Eucalyptus* stands, 750–

1020 stems/ha in the *Pinus* stands, and 720 to 930 stems/ha in the *Acacia* stands. Mean stand DBH was lowest for the *Acacia* stands, and those for the *Pinus* stands were within the range of those for the *Eucalyptus* stands. The *Acacia* trees generally had at least two trunks. Litter depth varied greatly among stands, and was greatest in the *Pinus* stand in each of the study areas. No effect of eucalypt age on litter depth was found.

3.2. Ordination of stands and species

As indicated in the correspondence analysis of the stands (Fig. 1), axis 1 separates the two study areas, whereas axis 2 separates the stands according to the abundance of the woody species. The eucalypt stands at Pointe-Noire are grouped to-gether, while the pine and acacia stands are located between the eucalypt stands and the secondary forest stand. The savanna stand is located close to the younger or disturbed eucalypt stands.

In the species analysis (Fig. 2), correspondence analysis results were very similar. Axis 1 separates those species restricted to the Pointe-Noire study area (lower values) from the species restricted to the Loudima study area (higher values). The intermediate species are present at both sites. The distance between the extreme values measures species preference for either one or the other study area. Axis 2 separates the species according to their natural habitats. In the

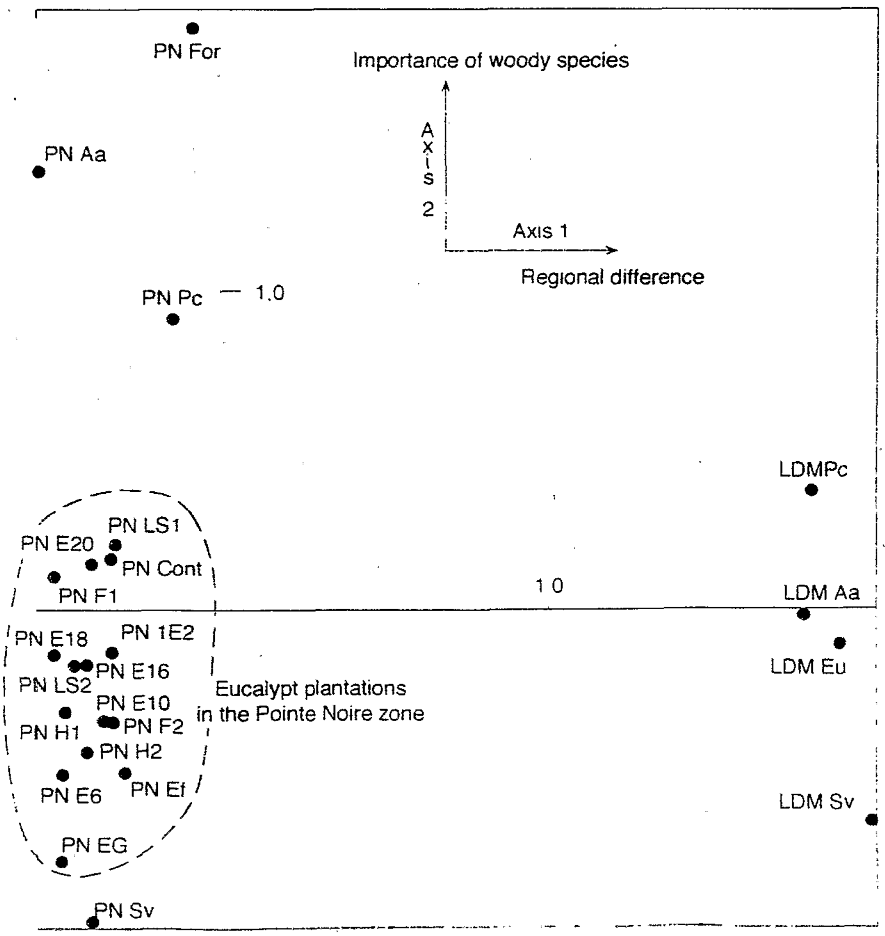

Fig. 1. Correspondence analysis for all plots (based on presence/absence of species present in at least two sites).

Pointe-Noire region, species with lowest values are those present in the savanna plots, and those with highest values in the forest.

3.3. Comparison of species richness at Pointe-Noire and Loudima

A total of 285 species were recorded in the two study areas: 215 in the Pointe-Noire study area and 108 species in the Loudima study area. Less than 20% of the species were present in both study areas. Each study area was found to have a unique flora. The number of species recorded in each stand is given in Table 3, and a full listing of species surveyed in each of the stands is presented in Tables 4, 5 and 6.

Floristic differences between the two areas were quite apparent, as shown in Figs. 1 and 2, and Table 4. In the savanna, the dominant grasses were *Loudetia arundinacea* in Pointe-Noire and *Hyparrhenia diplandra* in Loudima. The number and stem density of woody species was higher in Loudima than Pointe-Noire. The plantation understories in the pine, acacia,

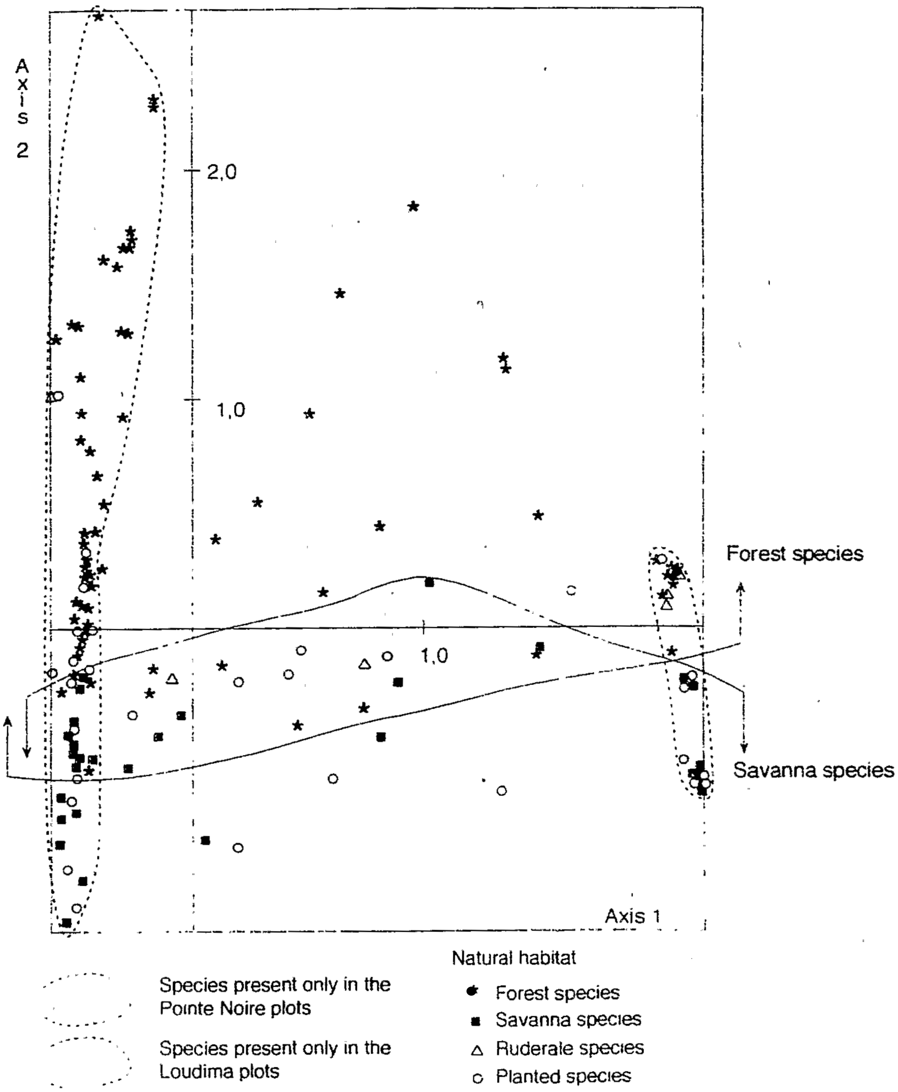

Fig. 2. Correspondence analysis for species (based on presence/absence of species present in at least two sites).

and older eucalypt stands were characterized by *Barteria nigritiana* or *Psychotria* cf. *peduncularis* in the Pointe-Noire area and by *Rauwolfia vomitoria* or *Diodia latifolia* in the Loudima site. The abundance of the spreading invader plant *Chromolaena odorata* was also noticeable in all Loudima plots.

The total number of species per stand (Table 3) was higher at Loudima than at Pointe-Noire for the eucalypt and acacia plantations, but similar between sites for pine plantations. Increased species richness in the Loudima stands relative to those at Pointe-Noire ranged from 9–10 species/stand in acacia and savanna stands to 23–32 species/stand in eucalypt plantations.

Regarding the natural habitats types (Table 3), only preliminary site comparisons are possible due to the low number of sites surveyed and the lack of floristic data for natural forests at Loudima. Excluding the Pointe-Noire natural forest plot, there do not appear to be any differences in the proportions of forest, savanna, ruderal, and planted species found in the two localities. The observed floristic differences between the two sites are probably due mainly to regional and/or edaphic factors.

3.4. Species richness at Pointe-Noire

Regarding the number of species found within the study areas at Pointe-Noire, the plantations were generally intermediate between savanna and forest. The sampling methodology used in this study was designed for plantation and savanna stands; since the natural forest vegetation was much more variable than either the plantations or savanna, its florisitic richness was therefore probably underestimated with the small number of replicate study plots used ($n = 6$, total sampling area = 471 m^2).

Plantation stands contained some species in their understories which where recorded in natural forest

Table 3

Number of species in the studied stands according to their natural habitats, and total species number

Stand	Plot name	Natural habitat of species				Total no. of species
		Forest	Savanna	Ruderal	Planted	
Pointe Noire						
Savanna	PN Sv	0	17	7	0	24
Eucalyptus	PN E6	7	12	5	0	24
Eucalyptus	PN E10	10	5	2	0	17
Eucalyptus	PN E12	19	4	1	1	25
Eucalyptus	PN E16	19	7	7	2	35
Eucalyptus	PN E18	18	7	1	0	26
Eucalyptus	PN E20	23	3	2	1	29
Eucalyptus	PN Ef	13	9	6	0	28
Eucalyptus	PN EG	7	8	6	0	21
Eucalyptus	PN Cont	29	9	10	0	48
Eucalyptus	PN H1	14	10	9	0	33
Eucalyptus	PN H2	14	7	14	1	36
Eucalyptus	PN F1	21	12	10	0	43
Eucalyptus	PN F2	11	12	5	1	29
Eucalyptus	PN LS1	30	7	12	1	50
Eucalyptus	PN LS2	14	9	7	1	31
Pinus	PN Pc	33	5	10	0	48
Acacia	PN Aa	15	0	2	1	18
Natural forest	PN For	95	0	2	0	97
Loudima						
Savanna	LDM Sv	1	15	18	0	34
Eucalyptus	LDM Eu	30	11	14	4	59
Pinus	LDM Pc	29	8	7	3	47
Acacia	LDM Aa	19	0	5	3	27

Table 4

Main plant species occurring in savanna, acacia, pine, and older eucalypt plantations at Loudima (LDM) and Pointe Noire (PN); species present in >50% of 78.5 m^2 sample plots in one or more stands

Species	Type	LDM Sv	LDM Eu	LDM Pc	LDM Aa	PN Sv	PN E20	PN Pc	PN Aa
Trees									
Acacia auriculiformis	T-P				+				
Barteria nigritiana	T-F						++	++	++
Gmelina arborea	T-P		++	++	*				
Milletia laurentii	T-P		*	++					
Sapium cornutum	T-F			++					
Shrubs									
Alchornea cordifolia	S-F			*	*		+		
Annona arenaria	S-S	++	++	*		*	++		
Bertiera cf. *batesii*	S-F						++	++	
Bridelia ferruginea	S-S	*	*	+					
Chromolaena odorata	S-R	+	++	++	++			*	
Lantana camara	S-R	*	++	*	*			*	
Macaranga spinosa	S-F		++	*	*		*		
Milletia versicolor	S-S	+							
Nauclea diderrichii	S-F		*	++					
Psorospermum tenuifolium	S-F						++	+	
Psychotria cf. *peduncularis*	S-F						++	++	++
Rauwolfia vomitoria	S-F		++	++			*	*	
Syzygium guineense	S-F							+	
Tarenna soyauxii	S-F								++
Vitex madiensis	S-S	+	*						
Herbs and grasses									
Amorphophallus sp.	H-R	*	++	*					
Bulbostylis laniceps	H-S					++			
Cassia mimosoides	H-S					+			
Commelina benghalis	H-R							+	
Ctenium newtonii	H-S					++			
Cyanotis lanata	H-S					++			
Cyperus amabilis	H-S					++			
Cyperus tenax	H-S					–			
Diodia latifolia	H-F		+	+	++			+	
Elionurus argenteus	H-S					++			
Eriosema erici-rosenii	H-S	++				++	*		
Hyparrhenia diplandra	H-S	++	+	*		*		*	
Hypoxis cf. *angustifolia*	H-A	+	++	*		*		*	
Imperata cylindrica	H-R	*	+						
Loudetia arundinacea	H-S					++			
Mariscus sumatrensis	H-S	*						+	
Oplismenus hirtellus	H-F		++	++					
Schyzachyrium platyphyllum	H-S	++	++						
Scleria boivinii	H-R					+		*	
Setaria chevalieri	H-S	+	*						
Climbers									
Cissampelos owariensis	C-F		+	*				+	
Dioscorea praehensilis	C-F		*	+					
Dioscorea sp. 2	C-F+				+				
Dioscorea sp. 1	C-F		++	++	*				

Table 4 continued

Species	Type	LDM Sv	LDM Eu	LDM Pc	LDM Aa	PN Sv	PN E20	PN Pc	PN Aa
Momordica charantia	C-R							+	
Premna lucens	C-F						++	+	++
Sabicea venosa	C-F							+	

Column 2: First letter indicates life form: C = climber, H = herb, S = shrub, T = tree. Second letter indicates natural habitat: F = forest, P = planted, R = ruderal, S = savanna. Columns 3–10: ++, present in >75% of the 78.5 m^2 sample plots; +, present in 50–75% of sample plots; *present in <50% of sample plots.

and savanna plots, as indicated in Tables 4 and 5. For example, the savanna plots contained 24 species, of which most were found in plantations stands (Table 7). Only two species were restricted to savanna plots, whereas the shrub *Annona arenaria* and some grasses like *Loudetia arundinacea* or *Elionurus argenteus* are widely spread in plantations. In contrast, approximately 75% of the species found in the forest plots were not found in either the plantation or savanna plots (Table 7). The most widespread forest species were pioneer species, *Premna lucens*, a climbing shrub, and some bushes or shrubs (*Psychotria* cf. *peduncularis*, *Chaetocarpus africana*, *Bertiera* cf *batesii*, *Rauwolfia vomitoria*). Only one species, *Scleria boivinii*, an opportunistic herb, was present in both the forest and savanna plots.

3.5. Effect of plantation parameters on understory species richness at Pointe-Noire

3.5.1. Age of Eucalyptus stands

Within the range of plantation ages studied (6–20 years: stands PN E6-PN E20), some stand characteristics remained constant with increasing age, such as canopy density which was always light, while others increased slightly, such as basal area which increased from 13 to 20 m^2/ha (Table 2). In the secondary forest plot, stand basal area (14.1 m^2/ha) was within the observed range in the eucalyptus plantation stands. Litter thickness in the *Eucalyptus* stands fluctuated with age from between 2.8 and 4.5 cm, whereas in the savanna, litter does not accumulate over time due to periodic burning, and in the natural forest it reached a maximum thickness of only 1.3 cm due to rapid litter decay.

The total number of plant species ranged from 17 to 35 among stands. For the eucalypt stands at Pointe-Noire, there was a tendency for the number of species to increase with stand age, but the relationship was not significant ($r = 0.288$, $P = 0.30$). A negative correlation was observed between stand age and the number of savanna species ($r = -0.579$, $P = 0.02$) and a positive correlation with the percentage of forest species ($r = 0.636$, $P = 0.01$). Some savanna species (mainly *Cyperaceae*) disappeared in the early years after planting, while *Annona arenaria* (a shrub) were still present in the oldest plantation. The forest pioneer species appear gradually: a first group including *Barteria nigritiana*, *Alchornea cordifolia*, and *Anthocleista nobilis*, which occurred in the 6-year-old plantation, whereas another group including *Chaetocarpus africanus*, *Rauwolfia vomitoria*, *Canthium* sp, *Psorospermum tenuifolium* appeared later in the 12-year-old plantation (stand PN E12).

3.5.2. Fire and herbicide effects on Eucalyptus plantations

The floristic composition of the control plot (PN Cont), where herbicide was not used and fire has not occurred for approximately two and a half years prior to sampling (since July 1993), was more similar to that of the natural forest plot than were plots which had been disturbed by fire or herbicide (figurehere>-Fig. 2). The application of herbicide or occurrence of fire reduced the number of understory species in the plantations when compared to the control stand (33, 36, and 48 species per stand in PN H1, PN H2, and PN Cont, respectively; Table 3). Further, the proportion of forest species decreased with herbicide treatment or fire relative to the control plot.

Fire strongly affects the floristic composition of plantation stands. In burnt stands, some grasses appeared (especially *Cyperus esculentus*, *Panicum brevifolium*, *Rhynchelytrum repens*) whereas they

Table 5

Main plant species occurring in eucalypt plantations of various ages, secondary forest and savanna at Pointe Noire (PN); species present in >50% of 78.5 m^2 sample plots in one or more stands

Species	Type	PN Sv	PN E6	PN E10	PN E12	PN E16	PN E18	PN E20	PN For
Trees									
Anthocleista nobilis	T-F		*	*	*	+	*	*	
Anthocleista sp. 2	T-F		*	++	+	+	++	++	
Barteria nigritiana	T-F								++
Carapa procera	T-F								
Pentaclethra eetveldeana	T-F								
Shrubs									
Agelea dewevrei	S-F								+
Alchornea cordifolia	S-F		*	++	+	+	++	+	
Annona arenaria	S-S	*	+	*	*	+	+	++	
Bertiera cf. *batesii*	S-F			+	+	+	++	++	*
Caloncoba welwitschii	S-F		*						++
Canthium sp.	S-F					++	*	*	*
Chaetocarpus africanus	S-F				*	*	*	*	++
Chromolaena odorata	S-R		++						
Cnestis urens	S-F								++
Coffea eketensis	S-F								+
Cola sp. 1	S-F								++
Dichostemma glauscens	S-F								+
Hymenocardia ulmoides	S-F								+
Leptactina manii	S-F						+	*	
Macaranga spinosa	S-F			+	++	*	++	*	
Microdesmis puberula	S-F								++
Phyllanthus sp.	S-F								+
Plagiostyles africana	S-F								++
Psorospermum tenuifolium	S-F				+	++	++	++	
Psychotria cf. *peduncularis*	S-F			*	++	++	++	++	*
Quassia africana	S-F								++
Rauwolfia vomitoria	S-F				*	*	*	*	+
Rhabdophyllum welwitschii	S-F								++
Rourea sp.	S-F								++
Uvaria sp.	S-F								++
Herbs and grasses									
Bulbostylis laniceps	H-S	++	*			*			
Cassia mimosoides	H-S	+	*						
Ctenium newtonii	H-S	++							
Cyanotis lanata	H-S	++	++						
Cyperus amabilis	H-S	++	*						
Cyperus tenax	H-S	+		*		*			
Elionurus argenteus	H-S	++	++				*		
Eremospatha sp.	H-F								+
Eriosema erici-rosenii	H-S	++	++	++	+	++	*	*	
Loudetia arundinacea	H-S	++	+	*	*	*	++		
Scleria boivinii	H-R	+	*						*
Climbers									
Gnetum africanum	C-F								+
Landolphia sp.1	C-F								+
Milletia comosa	C-F								+

Table 5 *continued*

Species	Type	PN Sv	PN E6	PN E10	PN E12	PN E16	PN E18	PN E20	PN For
Morinda morindoides	C-F								++
Premna lucens	C-F			*	++	++	++	++	*
Triclisia gilletii	C-F								+

Column 2: First letter indicates life form: C = climber, H = herb, S = shrub, T = tree. Second letter indicates natural habitat: F = forest, P = planted, R = ruderal, S = savanna. Columns 3–10: ++, present in >75% of the 78.5 m^2 sample plots: +, present in 50–75% of sample plots; *present in <50% of sample plots.

were absent in the control stand. Irrespective of the frequency of fire occurrence (two in PN F1, one in PN F2), fire had no significant influence on the distribution of species types (according to their natural habitats). Fire had a slight effect on species frequencies and only a few were noted: i.e., an increase for ruderal or savanna species as *Cyperus esculentus*, *Oldenlandia affinis*, and a decrease for the forest species *Anthocleista nobilis*.

Herbicide application appeared to favor grasses which were absent in the control plot (mainly *Cyperus esculentus*), but other effects were also noticeable. The frequency of some species was lowered (grasses such as *Loudetia arundinacea* or *Bulbostylis laniceps*, woody plants such as *Psorospermum tenuifolium* or *Bertiera* cf *batesii*), whereas other species did not seem to be affected (*Anthocleista nobilis* and *Barteria nigritiana*). *Psychotria* cf *peduncularis* is the only species to exhibit increased frequency with herbicide treatment. The time since herbicide application influences floristic composition. For example, stand PN H2, treated in January 1995, had slightly greater species diversity than stand PN H1, treated in April 1994. This difference was mainly due to a high number of savanna species in PN H2.

3.5.3. Effect of forest proximity to Eucalyptus plantations

The total number of species decreased from PN LS1 (10 m from the forest edge) to PN LS2 (50–100 m from the forest edge) (Table 3). A decreased percentage of forest species and an increased percentage of savanna species was associated with increasing distance from the secondary forest edge; no such trend was noted for ruderal species. Ten species found in the plot nearest to the forest edge (PN LS1) were also recorded in the natural forest stand, while only five species found in plot PN LS2 were also found in the natural forest (Table 6).

A total of 85 species included in the natural forest species list were not recorded outside of the forest plots. This number included species occurring at high frequencies in the natural forest stand: 22 of the 24 species found in at least in 50% of the natural forest plot replications were restricted to the forest. Only a few species recorded in the forest stand were found in the nearby plantation (forest species such as *Premna lucens* or *Maprounea membranacea*, ruderal species such as *Cogniauxia podolaena* or *Scleria boivinii*).These species occurred at low frequencies in the forest plots.

3.5.4. Effect of plantation density and planted species

Relative to lower density stands, the plantation stand with higher stem densities (1290 to 1600 ha^{-1} in PN Ef) had higher numbers of species (both total and forest species) and a lower percentage of savanna and ruderal species (Table 3). *Rauwolfia vomitoria* and *Canthium* sp. were the most noticeable forest species restricted to the high density plot. The stand with the lowest stem density (277 to 347 trees ha^{-1} in PN EG) showed higher densities for some heliophile species (*Cyperus amabilis*, *Psorospermum febrifugum*).

Comparison of *Pinus caribaea*, *Acacia auriculiformis* and eucalypt stands of similar ages (12 and 16 years old) indicated differences in their floristic composition, with the poorest flora found beneath acacia. Woody plant dominance, forest species proportion and ground cover were also highest in the *A. auriculiformis* stand. In the Pointe-Noire pine stands, undergrowth exhibited a very irregular pattern with dense patches scattered within undergrowth-free areas.

Table 6

Main plant species occurring in eucalypt plantations with various management interventions in the Pointe Noire study area (PN); species present in >50% of 78.5 m² sample plots in one or more stands

Species	Type	PN Con	PN F1	PN F2	PN H1	PN H2	PN Ef	PN EG	PN Ls2	PN Ls1	PN For
Trees											
Anthocleista nobilis	T-F	+	*	++	+	++	+	*	++	+	
Barteria nigritiana	T-F	+	+	+	+	+	+	+	++	++	
Carapa procera	T-F										++
Pentaclethra eetveldeana	T-F									*	++
Shrubs											
Agelea dewevrei	S-F										+
Alchornea cordifolia	S-F	+	*		+	*	++	+	+	++	
Annona arenaria	S-S	++	++	++	+	+	*		+	*	
Bertiera cf. *batesii*	S-F	++	*		+	+				+	*
Caloncoba welwitschii	S-F		*								++
Chaetocarpus africanus	S-F	*	*		*		*		*		++
Chromolaena odorata	S-R	*			++	*			*	*	
Cnestis urens	S-F										++
Coffea eketensis	S-F										+
Cola sp. 1	S-F										++
Dichostemma glaucescens	S-F										+
Hymenocardia ulmoides	S-F										+
Macaranga spinosa	S-F	+		*	++		*			*	
Maprounea africana	S-F	*	*						*	++	
Microdesmis puberula	S-F										++
Oldenlandia affinis	S-R	++	++	*	+	*	*	*	*	+	
Phyllanthus sp.	S-F										+
Plagiostyles africana	S-F										++
Psorospermum febrifugum	S-S						*	+			
Psorospermum tenuifolium	S-F	++	*	*	*	*			+	+	
Psychotria cf. *peduncularis*	S-F	*	*	*			+	+			
Quassia africana	S-F										++
Rauwolfia vomitoria	S-F	*					+				+
Rhabdophyllum weltwitschii	S-F										++
Rourea sp.	S-F										++
Uvaria sp.	S-F			**			*				++
Vernonia brazzavillensis	S-F	+		*					*	*	*
Herbs and grasses											
Andropogon gabonensis	H-S	*	+	*					*		
Asystasia gangetica	H-R	*	*		*	*	++	++		*	
Bulbostylis laniceps	H-S	++	++	++	+	*			++	+	
Cyperus amabilis	H-S	*	*	*	*	*	*	+	*	*	
Cyperus esculentus	H-R		++	*	+	*	++	++	*		
Dissotis cf. *rotundifolia*	H-R	*	*		*	*			*	+	
Elionurus argenteus	H-S	*	++	*	*	*	*	*	+	++	
Eremospatha sp.	H-F										+
Eriosema erici-rosenii	H-S	*		++	+		*	*			
Hypoxis cf. *angustifolia*	H-R	+		*	*				++	+	
Loudetia arundinacea	H-S	++	+	+	++	++			++	+	
Panicum cogoense	H-S	*	*	*					+		
Rhynchelytrum repens	H-S		*	*		*	++	+	*	++	
Rubiaceae	H-F				++	+		*			

Table 6 *continued*

Species	Type	PN Con	PN F1	PN F2	PN H1	PN H2	PN Ef	PN EG	PN Ls2	PN Ls1	PN For
Scleria boivinii	H-R	+				*				+	*
Climbers											
Gnetum africanum	C-F										+
Ipomea involucrata	C-R		++								
Landolphia sp. 1	C-F										+
Milletia comosa	C-F										+
Morinda morindoides	C-F										++
Premna lucens	C-F	++	++	+	++		++	+	*	++	*
Triclisia gilletii	C-F										+

Column 2: First letter indicates life form: C = climber, H = herb, S = shrub, T = tree. Second letter indicates natural habitat: F = forest, P = planted, R = ruderal, S = savanna. Columns 3–10: ++, present in >75% of the 78.5 m^2 sample plots; +, present in 50–75% of sample plots; *present in <50% of sample plots.

4. Discussion

4.1. Factors affecting plantation floristic composition

In both the Loudima and Pointe-Noire study areas, eucalypt, pine or acacia plantations do not inhibit colonization by native plant species. Allelopathy, shown previously to affect herb test plants (Bernhard-Reversat, 1991, unpublished), does not appear to affect native species after approximately ten years of litter and organic matter accumulation, an observation supported by studies in other tropical areas. In Ethiopia, Holgen and Svensson (1990) found that *Eucalyptus* plantation undergrowth was dominated by short grasses in a young stands, but in older (12-year-old) stands contained a very rich flora of climbers, shrubs and small trees). In Brazil, *Eucalyptus grandis* did not show any allelopathic effect on the many native species that colonize its understory in different regions (da Silva Junior et al., 1995). The results of the present study indicate that after 10 years, species richness of plantation understory vegetation exceeded that of the savanna. However, other studies have reported the absence of native vegetation in eucalypt plantation stands, a phenomenon attributed to allelopathy (Moral and Muller, 1969), particularly in the temperate zone (Alexander, 1989; Basanta et al., 1989; Madeira et al., 1989). Inter-specific variations in nutrient cycling by litter has also been found to affect soil fertility in plantations (e.g., Lugo et al., 1990).

The results of our study show that the plantation understory species were mainly woody species and that the understory floristic composition does change over time. Plantation age, density, and proximity to a natural forest stand are factors that favor increasing floristic diversity and development towards native secondary forest. Other parameters studied indicate that this development is slowed by disturbance factors including fire, herbicide use and other plantation weeding practices.

An increase in both total number of species and proportion or number of forest species was observed with increasing stand age. This was particularly noticeable after 10 years, whereas in younger plantations the understory vegetation was composed mainly of savanna-type species. The effect of proximity to the forest does not seem to be important beyond approximately 50 m. Plantation density also had little effect, considering that increasing density by a factor of 3.7 to 5.7 resulted in few changes in understory floristic composition.

The most important management practice in industrial plantations during the first 2 or 3 years after planting is weeding. Plantations in this study were mechanically weeded between the lines and manually weeded within the lines to prevent the development of a dense woody understory. The floristic analyses point to a notable increase of ruderal species to the detriment of forest species associated with weeding. However, woody plants which are able to regenerate vegetatively through stump sprouts can survive such weeding. The recently introduced practice of Chemical weed control has been recently introduced to reduce the savanna grass layer and minimize water competition with the eucalypts. Its effects on undergrowth is similar to that of other weeding techniques: i.e., a decrease in savanna species and an increase in the number of ruderal species.

The effects of fire on tropical savanna vegetation have been widely studied in the past, and fire is known to be the main agent responsible for maintaining savanna vegetation and preventing the establishment of forest species (Menaut et al., 1990). In the study sites, savanna species were particularly favored by fire: Sprouting woody species were able to regrow after light fires, as evidenced by the numerous young sprouts of *Psychotria* cf *peduncularis* were observed in burnt areas.

Table 7
Number of savanna and secondary forest species occurring in plantation stands at Pointe-Noire study site

Number of plantation stands[a]	Number of species	Cumulative percent
Species listed in savanna plot		
0	2	8
1	2	17
2	4	33
3	3	46
6	4	63
8	3	75
9	1	79
10	1	83
11	2	92
12	1	96
14	1	100
Species listed in forest plot		
0	72	74
1	8	82
2	4	87
3	3	90
4	1	91
5	2	93
6	2	95
7	1	96
11	2	98
12	1	99
15	1	100

[a]Plantation floristic lists were compared with those of savanna and forest plots; figures in column 1 indicate total numbers of plantations stands containing savanna or forest species. For savanna species, 2 species were not found in any plantation plots, 2 other species were found in 1 plantation plot, 4 other species were found in 2 plantation plots, etc. For secondary forest species, 72 species were not found in any plantation plots, 8 other species were found in 1 plantation plot, etc.

The composition and growth rate of the plantation understory vegetation is influenced by the planted species, which act on understory micro-climate through canopy shading, and on soil fertility through quality and quantity of litterfall. The observed pattern of decreasing savanna species richness from eucalypt to acacia to pine might be related to the increase in canopy cover across these plantation types. Although some data on soil changes in the plantations are available (Bernhard-Reversat, 1996), the relationships between vegetation and soil in plantations are poorly understood and require further study. Particular attention should be given to *Chromolaena odorata*. This species was present in both study areas but with higher frequencies and densities in Loudima. When *Chromolaena* forms a continuous plant cover, the other species cannot develop and species richness is strongly reduced.

4.2. Trends in vegetation succession

Eucalypt plantations in the Congo are harvested by clearfelling at 6–7 years of age, by which time they do not have a consistent undergrowth. Woody plants generally begin to invade the understory of eucalypt plantations later (>12 years old), as was observed in the older stands. Although not studied here, it must be noted that when eucalypts are clearfelled, the regrowth of understory vegetation is much more rapid than in the first rotation plots. This rapid regrowth may be related to the timber harvesting operation itself. Few seeds are introduced to the soil seedbank during the first rotation (Loumeto, 1996, unpublished data). Although plantation management for wood production is not intended to enhance the development of native vegetation, the present study demonstrates the ability of eucalypt plantations to contribute to the establishment of native species, mainly forest species. Therefore, the statement that

Eucalyptus plantations 'sterilize the soil' and prevent vegetation growth must be re-examined, taking into account the longer term changes.

Life-forms, seed dispersal strategies and vegetative reproduction abilities are important factors influencing understory establishment (McIntyre et al., 1995). These factors were not examined in detail in the present study. Nevertheless, considering only the main woody species encountered in this study, wind apparently plays an important role in seed dispersal, as many of them are known to have dry or small fruits, either achenes (in *Vernonia*) or capsules (in *Alchornea*, *Asystasia*, *Chromolaena*, *Leptactina*, *Macaranga*, *Maprounea*, and *Rauwolfia*). The birds which are found in plantations (Brosset, 1996; Bernhard-Reversat, 1996) are assumed to be important seed dispersal agents for the regeneration of *Euphorbiaceae* and *Rubiaceae*. The bird 'soui-manga' (*Nectarina cuprea*), although not listed in natural forests by Dowsett-Lemaire (1991), was very abundant in old plantations (Brosset, 1996) and could be involved in the pollination and seed dispersal of *Anthocleista* and *Psychotria*.

Once established, the plantation understory has a quite different floristic composition than that of the nearby natural secondary forest. Many species found in the forest plots are absent from the plantation stands. Some of the forest species of plantations are light-demanding species from edges and gaps in the *Symphonia* -dominated forest (Dowsett-Lemaire, 1991). The forest-like regeneration within the plantations is a unique plant community, and may be considered an early-regrowth forest, at an initial stage of secondary forest succession, as indicated the low numbers of species. The more typical secondary forests in the region are usually characterized by the presence of *Musanga cecropioides*, but this species was never observed in plantations in spite of the proximity of seed sources and disseminating bats noted by Brosset (1996).

The general trend of forest progression in savanna areas where fires are excluded has been described for many regions in the Congo, generally in uninhabited areas (Koechlin, 1961; Foresta, 1990; Schwartz et al., 1990; Schwartz, 1991; Schwartz et al., 1996; Hecketsweiler and Mokoko Ikonga, 1991; Doumenge, 1992) and in other regions of Central Africa or tropical moist Africa (Boulvert, 1990; Maley, 1990; Guelly et al., 1993; Achoundong et al., 1996). This forest regeneration is related to a moist climatic cycle but is destroyed by savanna fires. Therefore, protection from fire by management of tree planta tions would favor the establishment of forest species.

The future course of understory vegetation development is open to speculation, as neither data on vegetation development without undergrowth felling at the time of harvest, nor data on fire-protected savanna, are available. The negative impact of any kind of disturbance suggests that the plantation undergrowth will retain an important proportion of savanna species and will continue to be invaded by many ruderal species.

5. Conclusion

Open savanna areas which are either unused or under-utilized by local people acquire greater value through tree plantation establishment, which provide an economic activity and seems also to contribute to biodiversity restoration of poor lands. Despite the '*Eucalyptus* controversy', fast-growing tree species do contribute significantly to the social/rural economies in some countries, as in the case of eucalypts plantations in Cameroon (Gautier, 1994). There is therefore a good case for promotion of social forestry to meet population needs for firewood and construction wood, in addition to experimental and industrial plantations, especially in unused land such as savanna in the Congo (Loumeto, 1994).

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