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Effects of remnant trees in fallows on diversity and structure of forest regrowth in a slash-and-burn agricultural system in southern Cameroon

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ABSTRACT. Remnant trees in fields may facilitate regeneration in fallows by attracting seed dispersers and creating favourable sites for plant establishment. Ntumu shifting cultivators in Cameroon clearing rain forest spare some trees to provide shade for crops. This study examines their effects on regeneration by comparing vegetation in quadrats beneath and away from their crowns, in fallows of varying age (3–20 y). For fallows of all age classes, plant diversity was not significantly different between positions. Trees accounted for larger proportions of species and stems beneath remnant trees. Herbs, principally large monocots, accounted for larger proportions away from trees. Basal area was much higher in quadrats beneath trees. In all quadrats, the majority of individuals belonged to species with animal-dispersed seeds. These accounted for a larger proportion of individuals beneath trees (75%) than away (64%). Wind-dispersed species accounted for a larger proportion of stems away from trees (23.6%) than beneath (11.7%). These data suggest that enhanced seed rain by attraction of perching animals, demonstrated in a companion study, influenced regeneration patterns. Effects on regeneration were similar beneath trees of an animal-dispersed (*Pycnanthus angolensis*, Myristicaceae) and a wind-dispersed (*Triplochiton scleroxylon*, Sterculiaceae) species. Remnant trees in fallows may facilitate succession by nucleation, resulting in more rapid restoration of forest and conservation of nutrients in plant biomass.

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INTRODUCTION

Sparing isolated trees during clearing of fields is a common traditional practice in slash-and-burn agricultural systems of Central Africa (Bahuchet & De Maret 1993, De Wachter 1997, Dounias 1996). A number of studies in the New World tropics have shown that remnant or planted trees in fields, in regenerating pastures, or in plantation forests could favour the development of a 'nucleus of regeneration', both by providing favourable feeding and/or perching sites for forest seed dispersers and thereby enhancing seed rain (Cardoso da Silva *et al.* 1996, Guevara *et al.* 1986, 1992; Holl 1998, Janzen 1988, McClanahan & Wolfe 1993, McDonnell & Stiles 1983, Nepstad *et al.* 1996, Parrotta 1995, Vieira *et al.* 1994, Wegner & Merriam 1979) and by providing favourable conditions of light, moisture and nutrients for establishment of forest trees (Belsky & Canham 1994, Buschbacher *et al.* 1988, Nepstad *et al.* 1991, Vieira *et al.* 1994). Thus large isolated trees left in fields could allow forest species to establish earlier than in clearings of equal size but lacking such trees. These foci of regeneration of persistent species may eventually coalesce with others according to the model of succession by nucleation developed by Yarranton & Morrison (1974).

Thus far, studies of the effects of remnant trees on tropical forest succession have been done in the New World. These studies focus mostly on pasture recolonization or plantations in Mexico, Puerto Rico, Costa Rica and Amazonia (Aide et al. 1995, Cardoso da Silva *et al.* 1996, Guevara *et al.* 1986, 1992; Holl 1998, Nepstad *et al.* 1996, Parrotta 1995, Slocum 1997, Vieira *et al.* 1994). Abiotic conditions under trees, and their effects on establishment of other woody plants, have been studied in African savanna ecosystems (Belsky *et al.* 1989, Belsky & Canham 1994, Sirois *et al.* 1998). No studies of the role of remnant trees exist for African rain forests. Moreover, little is known, in either American or African forests, about how plant species richness and structure of regenerating vegetation change over time from 'abandonment' of the field to re-establishment of forest. The way in which succession is initiated determines the rate of regeneration and the structure of vegetation (Janzen 1988). The time of recovery of soil nutrient cycles depends on establishment of woody plants. Furthermore, the quantity of nutrients that can be made available to the next crop upon burning depends on how quickly they are stored in long-lived woody biomass.

The aim of this study was to analyse the differences in vegetation (diversity and structure) beneath the crowns of remnant trees that were spared during clearing of the field and patches away from such remnant trees in regenerating fallows, in a typical slash-and-burn agricultural system in southern Cameroon.

METHODS

The study site is described in more detail in the companion study on seed rain (Carrière *et al.* 2002).

Selected fallow sites

Field work, conducted in Nkongmeyos village (south-western Cameroon, 2°27′N, 10°27′E), was carried out during 3 mo (August–October 1997) at the beginning of the long rainy season. Seasonality is of the equatorial type and yellow ferralitic soils dominate the site; these are acidic and poor in nutrients (Letouzey 1985). Before recutting forest for another cycle of cultivation Ntumu farmers wait at least 10 y; fallow periods of 15–20 y are usual (Carrière 1999). This appears to be the time required by the soil and vegetation to recover most of its initial stock of nutrients. To sample regenerating vegetation, four replicates in each of three age classes of fallow (12 fallow fields) were selected. The age classes we defined were young fallows (3–5 y after the last weeding), middle-aged fallows (8–10 y) and old fallows (15–20 y). As a part of an 18-mo investigation of swidden agriculture (Carrière 1999), interviews (open-question methods, using cross-checking with different-aged cultivators) were conducted on the spot to establish age of different fallows in the village territory. It was impossible to identify fields with strictly identical histories of exploitation, but differences in history (frequency and intensity of slashing and burning and crop species cultivated) and in regenerating vegetation between fields of similar age were relatively small (Table 1).

Selected trees

Average area of Ntumu swidden fields was 0.81 ha and the sampled tree was in each case one of 3–7 large trees that had been spared in each field to provide, according to Ntumu farmers, light shade to crops (Carrière 1999). Field cartography (Carrière 1999) showed that usually no other small trees were left around a big tree spared in a field. Regrowth vegetation was sampled beneath and away from a total of 12 previously remnant trees, each located in a different field (all within an area of about 3 km^2 belonging to a single village), including six mature individuals each of *Triplochiton scleroxylon* K. Schum. (Sterculiaceae) and *Pycnanthus angolensis* (Welw.) Warb. (Myristicaceae) (Table 1). These two tree species were selected because of their high frequency in the fields, fallows and forest, and because they are also among the species preferentially left by cultivators during clearing (Carrière 1999). Trees selected were 30–45 m tall, their diameters ranged from 0.7 to 1.20 m and all had similarly broad crowns (15–25 m diameter). *Triplochiton scleroxylon* is a wind-dispersed species with high and dense crown foliage. The seed of *P. angolensis* is surrounded by an aril, and seeds of this species are dispersed by a variety of birds and mammals (Gautier-Hion *et al.* 1985). Crowns of *P. angolensis* are not very high and have relatively dense foliage. Based on results of previous studies indicating the importance of fleshy-fruited species as a magnet for seed-dispersing frugivores (Aide & Cavelier 1994, Gautier-Hion *et al.* 1985, Guevara & Laborde 1993, McDonnell & Stiles 1983), we hypothesized that fruiting *P. angolensis* might attract frugivorous vertebrates, in addition to simply serving as a perch, and might thus have a larger effect on seed rain than a tree that

Table 1. Characteristics of the selected fallows (E = 'egusi', *Cucumeropsis mannii* (Cucurbitaceae); P = peanuts, *Arachis hypogaea* (Fabaceae); C = cassava, *Manihot esculenta* (Euphorbiaceae); B = bananas, *Musa* sp. (Musaceae)).

Field number	Age class (y)	Times cultivated	Sampled trees		Land-use	Most abundant family (number of stems)	Most abundant family (number of stems)
			Triplochiton	*Pycnanthus*		Beneath trees	Away from trees
1	3–5	1	1		E	Acanthaceae	Araceae
2	3–5	2		1	E–P–C–B	Apocynaceae	Rubiaceae
3	3–5	1	1		E	Marantaceae Commelinaceae	Sterculiaceae
4	3–5	2		1	E–P–C–B	Commelinaceae	Asteraceae
5	8–10	1	1		E–P–C–B	Marantaceae	Sterculiaceae
6	8–10	2		1	E–P–C–B	Rubiaceae	Rubiaceae
7	8–10	2		1	E–P–C–B	Rubiaceae	Commelinaceae
8	8–10	1	1		E–P–C–B	Rubiaceae	Rubiaceae
9	15–20	2	1		E–P–C–B	Rubiaceae	Apocynaceae
10	15–20	2		1	E–P–C–B	Araceae	Liliaceae Rubiaceae
11	15–20	2		1	E–P–C–B	Fabaceae	Apocynaceae
12	15–20	2	1		E–P–C–B	Rubiaceae	Marantaceae
			n = 6	n = 6			

offers no reward to frugivores. Interviews showed that trees of this species are used as bird-attractive hunting sites and in the traditional pharmacopoeia. Their usefulness is given as the reason why they are spared during field clearing. During selection of trees, we confirmed by interviewing farmers that each individual tree of *Pycnanthus angolensis* selected (dioecious species) had borne fruits. In each fallow we sampled remnant trees that had been spared at each cycle of cultivation since the first clearing.

Sampling of fallow vegetation

For each of the 12 fields, representing two fields for each of the six possible combinations of tree species × age class of fallow, an individual tree was selected. For each of the 12 selected trees two quadrats (1.5 × 3 m) were located beneath the canopy of the remnant tree and two were placed at least 10 m beyond the border of its crown and at least 10 m from the crown of any other remnant tree in the same field. There was thus a total of 48 quadrats, 24 beneath and 24 away from the crowns of previously remnant trees. All plants rooted within the quadrat were recorded and height and dbh (diameter at breast height) of the trunk of each was measured. Diameter of herbaceous stems at their base was also measured. Each plant was identified (to species, when possible) by examination in the field, and when necessary, by comparison with specimens in the Cameroon National Herbarium, Yaoundé. Life form (herb, herbaceous vine, woody vine, shrub, tree) of each plant was noted, and the origin of each individual stem (seed, clonal growth, or sucker sprouts from a live stump) was determined. As noted above, no small trees are left in the vicinity of large trees spared from felling. There was thus no confusion between remnant vegetation (only large trees, and sucker sprouts from trunks) and regrowth during the fallow. Interviews on the spot with the field owner were conducted to confirm this point. Sucker sprouts from stumps, and stems originating from rhizomes or stolons, were readily evident. In their absence the stem was scored as having originated from seed. For clonally growing plants, each individual stem was counted and its origin defined as vegetative propagation. Some stems could not be identified with precision, and these sometimes could not be classified as to life form. Overall, 54 stems of a total of 3756 sampled could not be identified with sufficient precision (family level) to be included in our analyses.

Data analysis

For each quadrat, we calculated the following: (1) total species richness. (2) Shannon diversity index: $I_s = -\Sigma\ (N_i / N) \times \log_2 (N_i / N)$, where N_i is the number of individuals of species i in a quadrat and N the sum of the number of individuals of all species in the same area (Magurran 1988). This index of diversity is particularly appropriate to our comparative study because it is independent of sample size. (3) Basal area per quadrat (4.5 m^2): BA (cm^2) = $\Sigma\ (C^2/4\ \pi)$, where C is the circumference (at breast height, except for herbs, which were measured at ground level) of each plant found in the quadrat (CTFT 1976). Although BA generally refers to woody species, we included in some of our calculations trees, shrubs, woody vines and herbaceous plants. This study addresses changes during a period (from 5–20 y of regrowth) in which non-woody species account for a considerable portion of biomass. Herbaceous plants are usually not included in calculation of BA by foresters, but we included them because some large monocotyledonous herbs, Marantaceae and Zingiberaceae, are frequent in understorey of secondary forest in Central Africa and affect dynamics of succession (White & Abernethy 1996). Their inclusion in the analysis is thus essential. BA was also analysed separately for each different life form, as well. BA is included to give a rough approximation of plant biomass production which usually increases with age. We excluded live stumps, made at field clearing, that bore sucker shoots because these do not reflect growth during the fallow period.

For each of these dependent variables, GLM procedures (General Linear Models, SAS 1996) were used to compare means and to test effects of the following predictor variables: (1) position of quadrats, beneath or away from remnant trees; (2) species of remnant tree; (3) age class of fallow. The GLM procedure included repeated-measures analysis of variance (SAS 1989, pp. 923–926, routine repeated examples pp. 982–986 and pp. 988–993) to test hypotheses for between-subject effects, and univariate tests of hypotheses for within-subject effects. Because the two positions are in the same field, there is a possible correlation between these two measures. Here repeated measures analysis corresponds to a split-plot design in which the field is analogous to a plot and the two positions are analogous to subplots. Because a group of four quadrats is associated with each tree (in each field), each quadrat cannot be considered an independent sample. For each location (beneath and away) means were calculated for each pair of quadrats. Variables were transformed before calculation of means. (1) Where analyses were conducted on percentages of counts, these variables (Y) were first transformed ($_{tr}$) such that Y_{tr} = arcsine ($Y^{1/2}$); (2) where analyses were conducted on percentage of measures (following a log-normal distribution), these were first transformed such that $Y_{tr} = \log(1+Y)$; (3) finally, on counts following a Poisson distribution, these were first transformed such that $Y_{tr} = Y^{1/2}$. In examining significance of results, we used type II sums of squares (SAS 1996). The different sources of variation were presented in Table 2. For the factor age of fallow, orthogonal contrasts were computed, so that linear effect and deviation from linear effect were

Table 2. Structure of the analysis with the different sources of variation and the degree of freedom (df).

Source of variation	df
Between-subjects effects	
Species	1
Age	2
Species × age (interaction)	2
Within-subjects effects	
Position	1
Position × species	1
Position × age	21
Position × species × age	27

tested, for each species (age × species interaction) and for general effect (age effect).

RESULTS

General description

A total of 307 species (3756 stems) was found in the 48 quadrats: 51 shrubs (895 stems), 117 trees (700 stems), 72 herbs (1331 stems), 56 climbers (662 stems of woody and herbaceous vines) and 11 morphospecies (444 stems), mostly represented by immature individuals, whose family and life forms could not be determined. Species sampled belonged to 78 families, the most richly represented being Rubiaceae and Euphorbiaceae (each with 19 species, Table 3), followed by Araceae, Apocynaceae and others (Table 3). All of these species-rich families include representatives of both mature- and secondary-forest species (Letouzey 1985). These most species-rich families did not always account for the largest numbers of stems (Table 3) in the 3–20-y-old fallows sampled. Thus Rubiaceae, Euphorbiaceae, Araceae and Apocynaceae accounted for the largest numbers of species, whereas Rubiaceae, Marantaceae, Commelinaceae and Euphorbiaceae accounted for the largest numbers of individual plants.

Table 3. The most important families found in the quadrats (total area sampled 216 m^2). The total corresponds to the whole quadrat sampling.

Plant family	n species	% of all species	stems	% of all stems
Rubiaceae	19	6.1	845	22.5
Euphorbiaceae	19	6.1	215	5.7
Araceae	17	5.5	191	5.1
Apocynaceae	16	5.2	206	5.5
Commelinaceae	10	3.2	234	6.2
Fabaceae	10	3.2	129	3.4
Moraceae	10	3.2	100	2.7
Marantaceae	9	2.9	325	8.6
Subtotal	110	—	2245	—
Total	307	100	3756	100

Number of species was under-estimated because not all individuals could be determined to species level.

Species richness

The sum of the number of species over all quadrats was 232 beneath and 215 away from the crowns of remnant trees; species richness was not significantly different beneath (20.5 ± 7.9) and away (20.6 ± 7.0) from the crowns of these trees (Table 4). Number of stems per quadrat ranged from 17 to 231 and number of species between 8 and 39. Shannon index for the 48 quadrats ranged from 1.03 to 4.76. Species richness and diversity index were not significantly affected by quadrat positions, age of fallow or species of remnant tree (Table 4).

Relative abundance and diversity of different life forms

The per cent of stems per quadrat that were shrubs (23.6% beneath and 21.0% away), herbaceous vines (8.6% beneath and 8.2% away), and undetermined life-forms (5.9% beneath and 3.9% away) did not differ significantly by position or any other predictor variables. In contrast, stems that were of trees (27.2% beneath and 15.2% away) and stems that were of non-climbing herbaceous plants (22.7% beneath and 37.4% away) were both significantly affected by position ($F = 8.4$, df = 1,6, $P < 0.03$ for tree stems and $F = 6.2$, df = 1,6, $P < 0.05$ for herbaceous stems). Under trees there were more trees and fewer herbs, while away from trees there were more herbs and fewer trees. For non-climbing herbaceous plants several effects other than position were detected: (1) a tree species effect ($F = 16.9$, df = 1,6, $P < 0.007$) and species × position interaction ($F = 6.40$, df = 1,6, $P < 0.05$) due to the larger number of herbaceous plants away from *Triplochiton scleroxylon* only (Figure 1a); (2) an age effect ($F = 9.53$, df = 2,6, $P < 0.02$) related to decreasing percentage of herbaceous plants with increasing age of fallow, especially away from remnant trees, and (3) a species × age interaction effect ($F = 5.20$, df = 2,6, $P < 0.05$) due to the decreased number of herbaceous plants with age of fallow beneath and away from *P. angolensis*, while beneath and away from *T. scleroxylon* this number decreased from young to middle-aged fallows, then increased slightly from middle-aged to old fallows (Figure 1a). Per cent of stems that were of woody vines increased with age of fallow (Figure 2a) both beneath (n.s.) and away ($F = 26.7$, df = 2,6, $P < 0.001$) from the crowns of trees. The linear effect of age was significant away from the crown in both species, but much stronger for *P. angolensis* ($F = 51.2$, df = 2,6, $P < 0.0005$) than for *T. scleroxylon* ($F = 10.1$, df = 1,6, $P < 0.02$). None of the predictor variables significantly affected percentage of species of shrubs, non-climbing herbaceous plants and herbaceous vines. Percentage of species as trees was significantly higher beneath than away from the crown of remnant trees ($F = 9.69$, df = 1,6, $P < 0.02$) while despite a tendency, the number of species of non-climbing herbaceous plants was not significantly higher away from the crown of remnant trees. The per

Table 4. Mean species richness and Shannon index per quadrat (4.5 m^2) for each species of remnant tree and in the three different age classes of fallows ('Beneath' is under the canopy and 'Away from' is in the open field; Young, Middle-aged and Old refer to the ages of fallows). For both estimates of diversity, none of the differences between locations, tree species, age classes of fallows, or combinations of these parameters, was statistically significant.

	Beneath	Away from
Shannon index	3.37 ± 0.6	3.29 ± 0.5
Mean species richness	20.5 ± 7.9	20.6 ± 7.0

	Beneath		Away from	
	Pycnanthus	*Triplochiton*	*Pycnanthus*	*Triplochiton*
Shannon index	3.21 ± 1.0	3.52 ± 0.3	3.47 ± 0.4	3.11 ± 0.6
Mean species richness	22.5 ± 9.8	18.6 ± 5.2	22.4 ± 7.8	18.9 ± 5.7

	Young		Middle-aged		Old	
	Beneath	Away from	Beneath	Away from	Beneath	Away from
Shannon index	3.66 ± 0.5	3.18 ± 0.6	3.22 ± 0.5	3.13 ± 0.2	3.23 ± 1.1	3.57 ± 0.2
Mean species richness	21.1 ± 9.2	24.0 ± 8.8	22.0 ± 9.4	17.5 ± 4.6	18.5 ± 5.0	20.5 ± 5.9

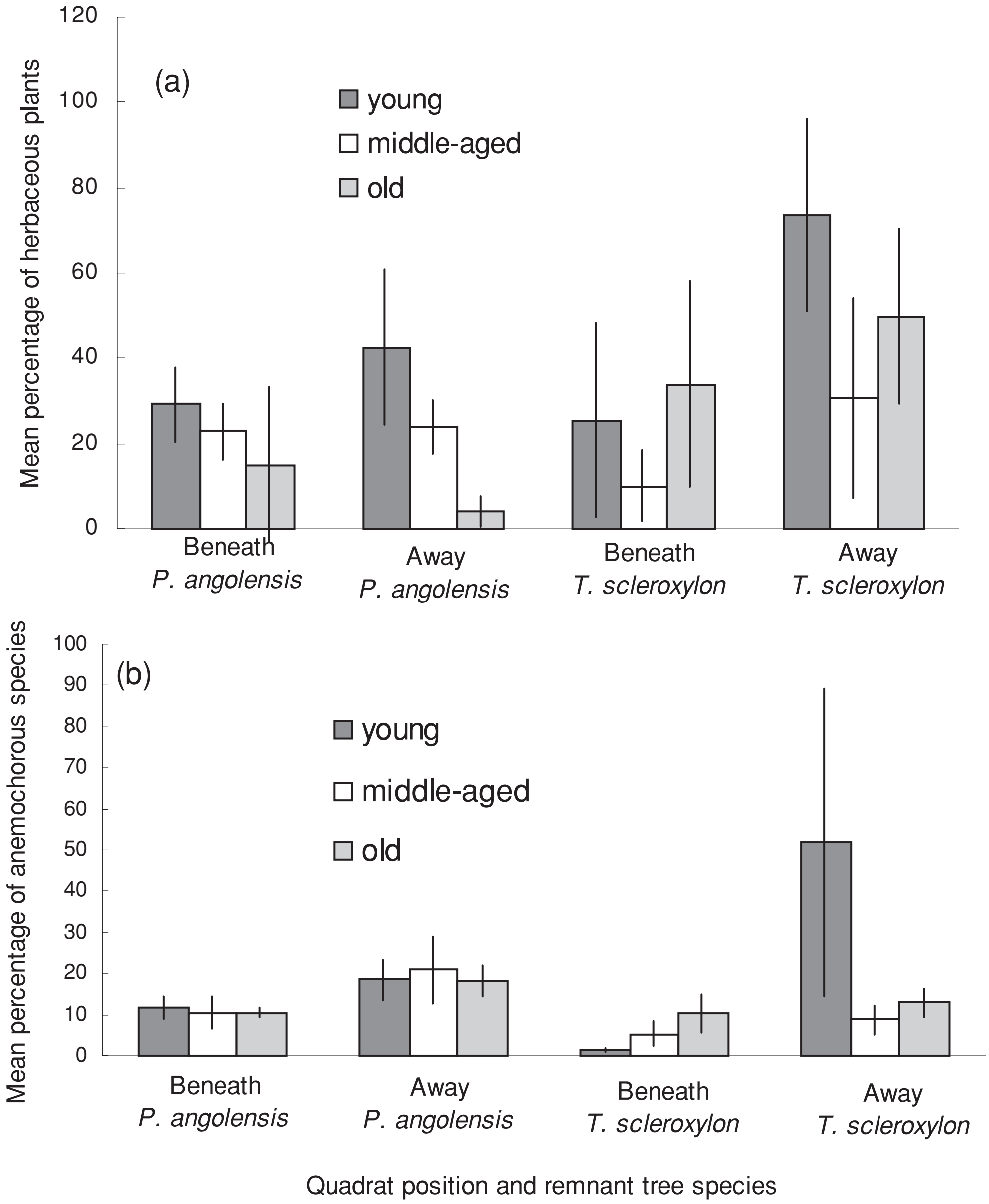

Figure 1. Mean percentage of individual stems (a) of herbaceous plants and (b) of wind-dispersed species beneath and away from the crown of *Pycnanthus angolensis* and *Triplochiton scleroxylon*. Bars represent means, lines represent standard deviation.

cent of stems that were of woody vines increased with age of fallow both beneath (n.s.) and away ($F = 11.4$, $df = 2,6$, $P < 0.01$) from the crown of trees. For both per cent of stems and of species that were of woody vines, a significant species × age interaction effect existed away from the crown of remnant trees.

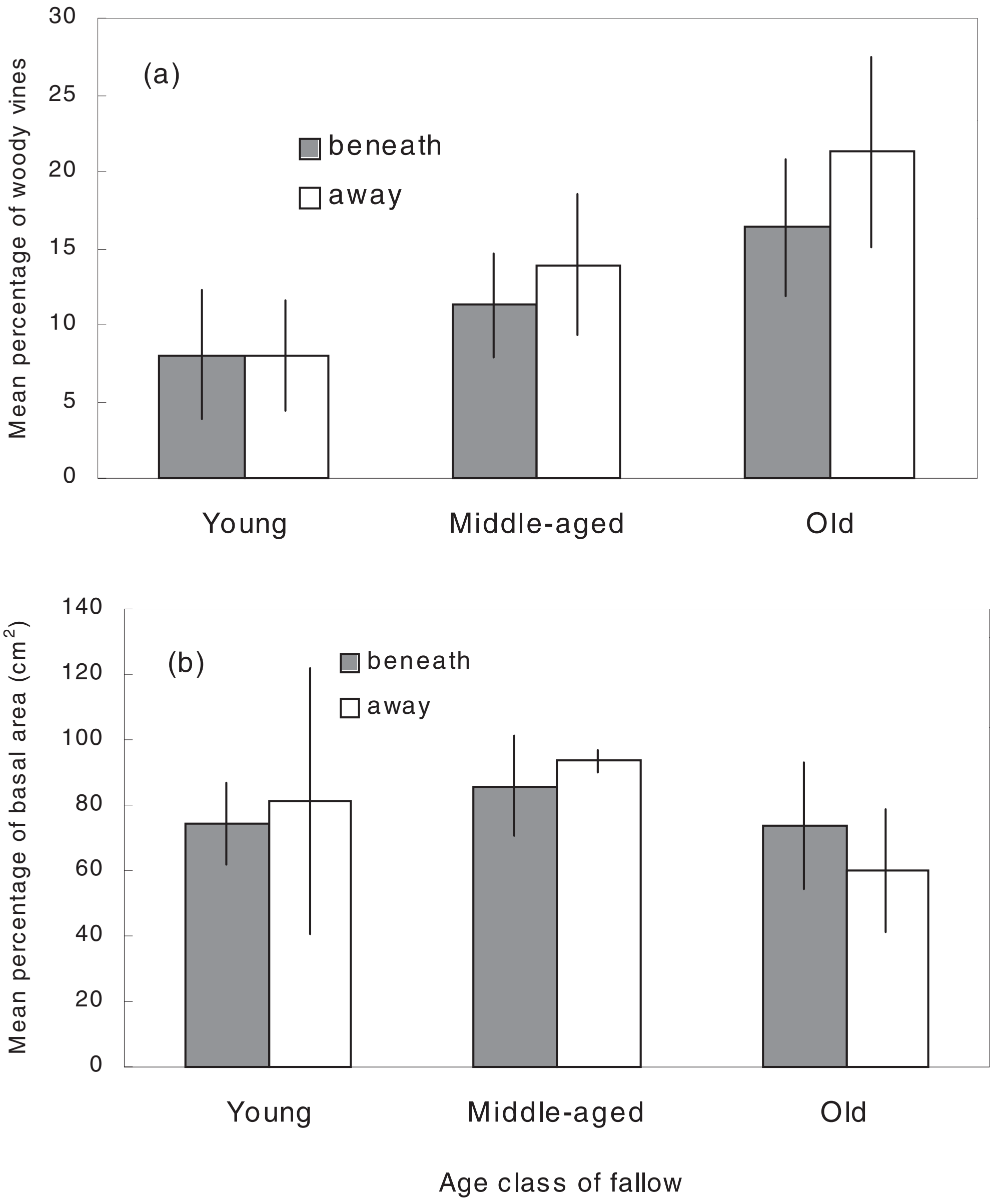

Figure 2. Mean percentage (a) of individual stems of woody vines and (b) of basal area (BA, cm^2) of animal-dispersed species beneath and away from the crown of remnant trees in different age classes of fallows. Bars represent means, lines represent standard deviations.

Basal area (BA)

Quadrat position had a strong and significant effect ($F = 19.2$, $df = 1,6$, $P < 0.004$) on the mean total BA (including all life-forms per quadrat). Mean total BA was higher beneath (885 ± 515 cm^2) than away (197.4 ± 127 cm^2) from the crowns of remnant trees. BA was mostly contributed by woody species (trees and shrubs) beneath (862 ± 210 cm^2) and to a lesser extent away (119 ± 36 cm^2) from the crowns. Individual trees and shrubs were larger beneath the crowns of remnant trees than away, and the size distribution of stems was more variable beneath remnant trees and relatively uniform away from remnant trees (Figure 3). Indeed, the eight largest diameter classes together represented only 1.4% (30 stems) of the total of individual stems away from the remnant trees, but 6.7% (108 stems) beneath remnant trees. For the two largest diameter classes stems belonged to rapidly growing pioneer species, such as *Myrianthus arboreus* P. Beauv. (Moraceae), *Macaranga hurifolia* Beille (Euphorbiaceae), *Musanga cecropioides* R. Br. (Moraceae), *Ficus vogeliana* Warb. (Moraceae), *Grewia* sp. (Tiliaceae), *Trema guineensis* (Schum. & Thonn.) Ficalho, and long-lived pioneer species such as *Funtumia elastica* (Preuss) Stapf (Apocynaceae), *Terminalia superba* Engl. & Diels (Combretaceae) and *Triplochiton scleroxylon* (Sterculiaceae). Interestingly, only four of these nine abundant species (*Musanga*, *Ficus*, *Trema* and *Terminalia*) were represented in the seed rain (Carrière *et al.* 2002).

When total BA is broken down into the different life forms, the per cent of BA accounted for by trees differed significantly by quadrat position (F = 8.69, df = 1,6, $P < 0.02$) and in a manner inverse to per cent of BA accounted for by non-climbing herbaceous plants (F = 17.3, df = 1,6, $P < 0.006$). BA of trees was higher beneath remnant trees, while BA of non-climbing herbaceous plants was higher away from remnant trees (Figure 4). BA of herbaceous plants decreased sharply and linearly with age of fallow (F = 15.4, df = 1,6, $P < 0.01$) beneath the crown of *P. angolensis*. BA of shrubs was higher away from the crown of *P. angolensis* than away from the crown of *T. scleroxylon* (F = 8.11, df = 1,6, $P < 0.03$). Finally, a significant linear effect (F = 9.71, df = 1,6, $P < 0.02$)

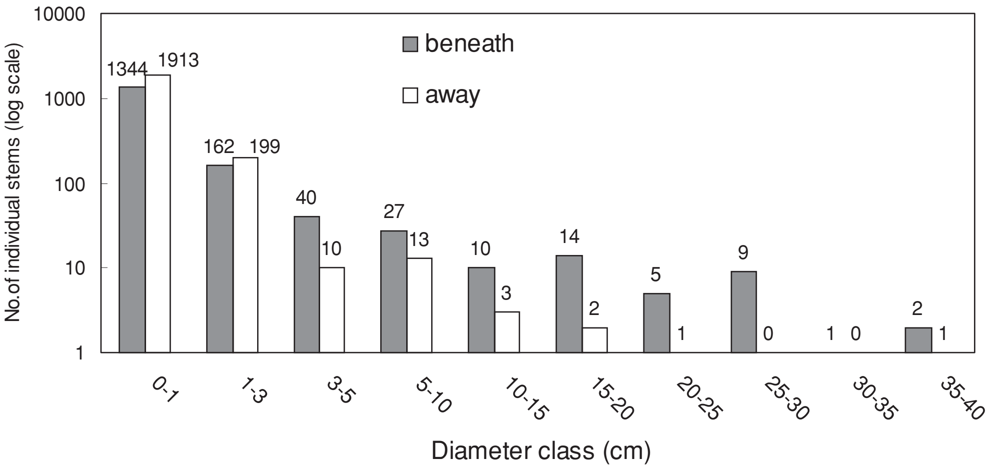

Figure 3. Total number of stems in different size-classes (diameter, cm) found in quadrats beneath and away from remnant trees in all age classes of fallows.

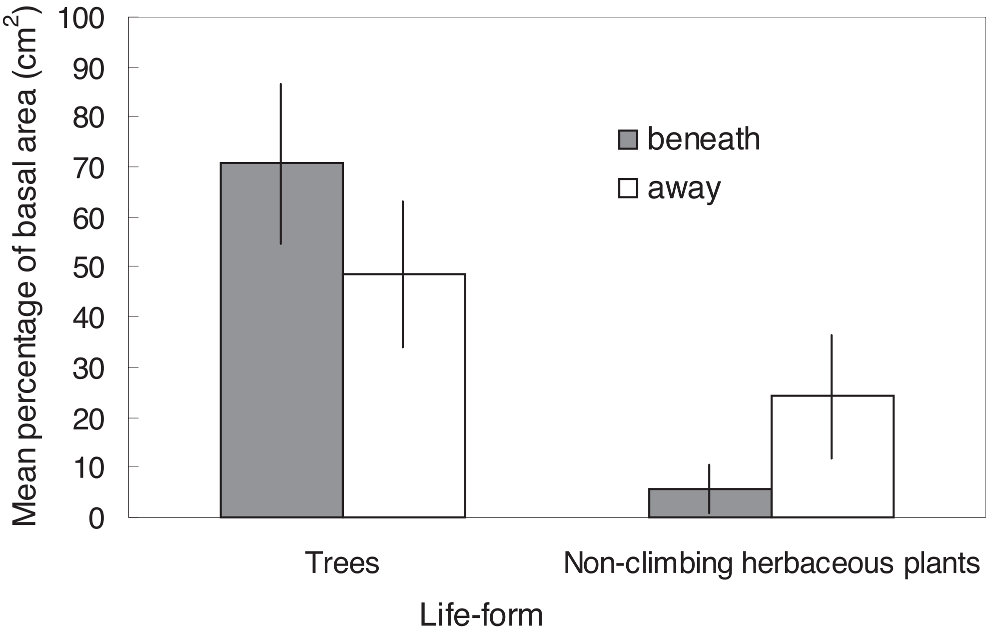

Figure 4. Mean percentage of basal area (BA, cm^2) of tree and non-climbing herbaceous life-forms beneath and away from the crowns of remnant trees. Bars represent means, lines represent standard deviations.

of age × species interaction on BA of woody vines was due to sites away from the crown of *P. angolensis*, where BA of woody vines increased linearly with age. BA was higher beneath crowns of isolated trees than away, in both middle-aged fallows and old fallows (Figure 5). BA of woody plants was responsible for this difference. Furthermore, BA increased with age of the fallow beneath crowns of remnant trees but not away from their crowns (Figure 5). There was no significant effect of age on the mean percentage of total BA, as well as on the mean percentage of BA for each life-form taken separately. This was due to the great variation among quadrats and the very high standard deviation.

The sum of BA over all 48 quadrats (216 m^2) sampled was 25 067 cm^2, of which 21 408 cm^2 was accounted for by quadrats beneath the crowns of these trees. Thus, although quadrats beneath trees accounted for half the total area sampled, they included 85.4% of total BA. Five tree species together accounted for over 50% of total BA beneath remnant trees: *Myrianthus arboreus* (Moraceae), 26.1%; *Macaranga hurifolia* (Euphorbiaceae), 7.9%; *Musanga cecropioides* (Moraceae), 6.7%; *Ficus vogeliana* (Moraceae), 6.3%; and *Grewia* sp. (Tiliaceae), 4.3%. Away from remnant trees, three species together accounted for over 50% of BA: *Musanga cecropioides*, *Trema guineensis* and *Funtumia elastica* (Apocynaceae). Herbs were of greater importance (number of stems and BA) in quadrats away from crowns of remnant trees. The most common herbs in the quadrats were *Aframomum citratum* (Pereira) K. Schum. (Zingiberaceae) and *Haumania danckelmaniana* (J. Braun & K. Schum.) Milne-Redh. (Marantaceae). If we add their

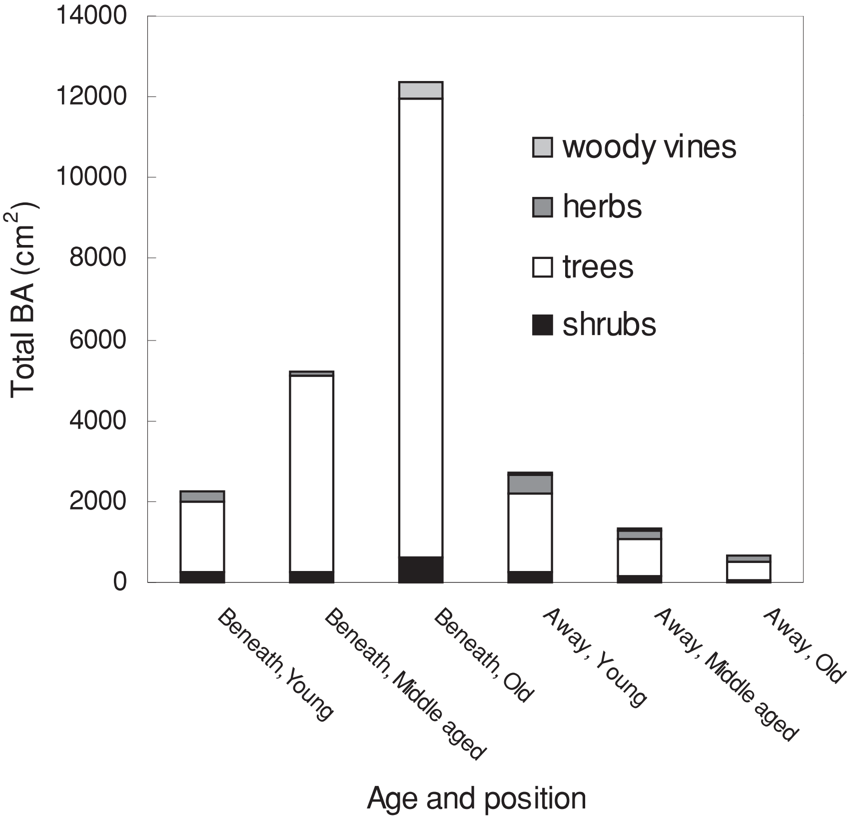

Figure 5. Total basal area (BA, cm^2) of woody vines, herbs, trees, and shrubs, beneath and away from the crowns of remnant trees in different age classes of fallows.

BA to that of trees and shrubs, these two species together represented 10% of the BA away from crowns of remnant trees and only 0.1% of BA beneath these trees. *Musanga cecropioides*, the most important early stage pioneer species in central African rain forests, represented 34.3% of the BA away from crowns of remnant trees and only 6.7% beneath crowns of these trees.

Dispersal mode

Beneath crowns of remnant trees, 75% of stems were of species with zoochorous seeds and only 12% of stems belonged to wind-dispersed species. Away from crowns of remnant trees, only 64% of stems were of species with zoochorous dispersal, and 24% of stems belonged to wind-dispersed species. Percentage of stems of wind-dispersed species differed significantly ($F = 5.99$, df = 1,6, $P < 0.05$) according to the position of quadrat. Percentage of stems of wind-dispersed seeds increased linearly and significantly with age beneath *T. scleroxylon* ($F = 7.79$, df = 1,6, $P < 0.03$; Figure 1b). However, percentage of wind-dispersed plants beneath remnant trees in old fallows was comparable to percentage of wind-dispersed plants away from the crowns of remnant trees in young fallows (Figure 1b). Percentage of wind-dispersed species was higher away from the crowns of remnant trees ($F = 5.94$, df = 1,6, $P < 0.05$), while percentage of animal-dispersed species was higher beneath remnant trees ($F = 6.41$, df = 1,6, $P < 0.05$). BA of animal-dispersed species showed a significant age effect away from the crowns of remnant trees ($F = 6.86$, df = 2,6, $P < 0.03$; Figure 2b). Basal area of animal-dispersed species was less variable over time beneath remnant trees than away from remnant trees (Figure 2b).

Origin of stems

Mean percentage of stems originating from germination of seed showed a non-significant trend to be higher beneath (75.7%) the crown than away (68.6%) from the crown of remnant trees. Stems originated from seed were relatively more numerous beneath *T. scleroxylon* and less numerous away from the crown of this species only ($F = 10.5$, df = 1,6, $P < 0.02$). In both positions, for trees of both species taken together, the per cent of the total BA accounted for by stems that originated as seedlings (Figure 6) was significantly higher beneath (89.8%) than away from (72.3%) remnant trees ($F = 29.9$, df = 1,6, $P < 0.002$). A significant position × age interaction effect ($F = 5.39$, df = 2,6, $P < 0.05$) was also detected (Figure 6). The BA contribution of individuals originating from seeds was lower away from the crowns of remnant trees than beneath remnant trees of both species. In contrast, percentage of stems originating from vegetative propagation was significantly ($F = 8.41$, df = 1,6, $P < 0.03$) higher away

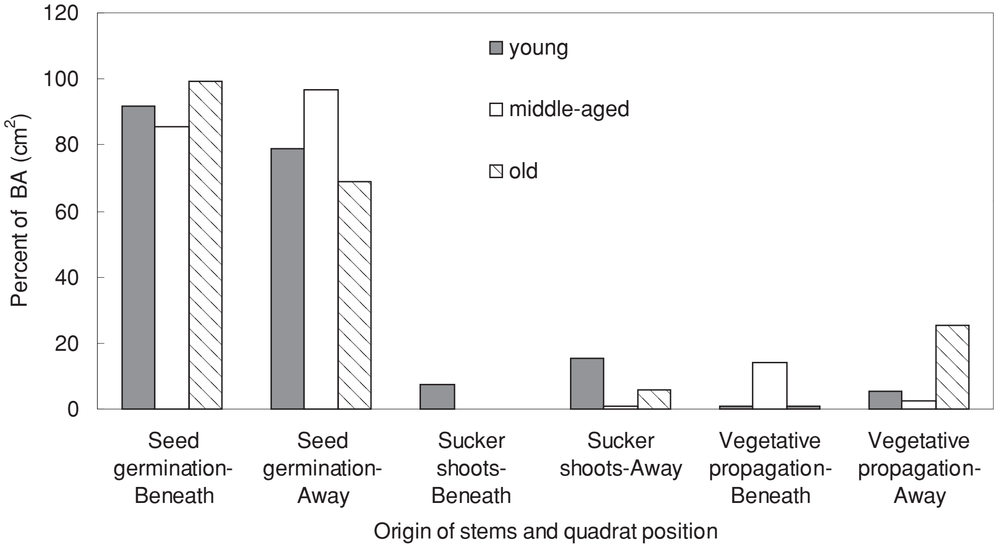

Figure 6. Per cent of BA (cm^2) of individual stems that originated from seed germination, sucker shoots and vegetative propagation, beneath and away from the crowns of remnant trees of both species taken together in different age classes of fallows.

(28.3%) from than beneath (19.7%) the crowns of remnant trees. Number of stems originating from vegetative propagation was higher away from the crown than beneath for remnant *T. scleroxylon*, while this number decreased slightly from beneath the crown of *P. angolensis* to away from the crown of this species (F = 15.6, df = 1,6, P < 0.01). Percentage of BA accounted for by stems produced by vegetative propagation was greater away from (20.2%) than beneath (4.1%) remnant trees (F = 6.79, P < 0.04). Different patterns with age were observed for BA accounted for by vegetative propagation beneath and away from *T. scleroxylon*, contrasting with a general increase of BA accounted for by this source, both beneath and away from *P. angolensis* (position × age × species interaction; F = 6.44, df = 2,6, P < 0.04). Sucker shoots from live stumps accounted for a small number of stems. A strong age effect was detected (F = 24.0, df = 2,6, P < 0.002) beneath remnant trees. Percentage of sucker shoots decreased dramatically and linearly over successive fallow age classes beneath the crowns of remnant trees (F = 27.1, df = 1,6, P = 0.002). The same strong age effect beneath remnant trees was detected (F = 34.1, df = 1,6, P < 0.0005) for percentage of BA accounted for by sucker shoots (Figure 6). A significant species effect (F = 10.4, df = 1,6, P < 0.002) was due to the fact that a higher percentage of BA was accounted for by sucker shoots beneath and away from the crowns of *P. angolensis* than beneath and away from those of *T. scleroxylon*.

DISCUSSION

Succession and changes in vegetation structure

Establishment of woody plants, especially those that persist in later successional stages such as *T. scleroxylon*, *Terminalia superba* and *Ficus* spp. (Letouzey 1985), was enhanced under the canopies of remnant trees in fallows. Our results show that this effect was due to faster growth rates of long-lived woody species beneath their crowns. Away from the crowns of these trees, both lower seed rain and abiotic conditions favoured the establishment of clonally growing, light-demanding monocotyledonous herbs. The abundance of large herbaceous monocots, especially Marantaceae and Commelinaceae, in patches in these fallows reflects the common occurrence of these large herbs in some types of secondary vegetation in central Africa (White & Abernethy 1996). In Central Africa fallows are dominated by the most common pioneer species, *M. cecropioides*, and to a lesser extent by *Trema guineensis*, *Macaranga* spp. and *Myrianthus arboreus* (Letouzey 1985, Mitja & Hladik 1989). Usually *Musanga* dominates regrowth in sites cleared for the first time and *Trema* dominates in sites burned multiple times (Mitja & Hladik 1989). Despite higher *Musanga* seed rain beneath remnant trees (Carrière *et al.* 2002) the present study showed that *Musanga* stems were more abundant away from the crowns of remnant trees while *Trema* was not more common in the absence of *Musanga*, either beneath or away from the crowns of remnant trees. This suggests that the fallows we studied had in general not been cultivated over many cycles or burnt several times, and that sites beneath remnant trees generally short-cut the first pioneer stage of *Trema* or *Musanga*.

Diversity

Remnant trees in agricultural landscapes are preferred perching sites for forest birds and mammals, greatly enhancing the abundance and diversity of seed rain. In contrast to findings elsewhere (e.g. Guevara *et al.* 1992), in this study, despite a tendency to higher diversity beneath remnant trees, plant diversity was not significantly greater in quadrats located beneath crowns of remnant trees than in quadrats away from the crown of such trees. Composition of vegetation was thus not a simple reflection of more diverse seed rain beneath trees. Differences in the biotic and abiotic environment between sites beneath and away from remnant trees could lead to differential regrowth (Nepstad *et al.* 1996, Vieira *et al.* 1994); competition, predation and other processes could counter any overall effect of seed rain on species diversity, at least at the local scale of small quadrats. Effect of greater seed rain on species diversity at a larger spatial scale is likely to be quite different.

Basal area (BA) and biomass production

BA of woody stems, which reflects biomass accumulation during regeneration, was greater beneath remnant trees than away from the crowns of remnant trees in fallows. Beneath these trees, woody stems were more numerous and stems were both larger on average and more variable in size. Many studies have demonstrated that environmental conditions beneath remnant trees, planted trees, or plantation forests are favourable to the establishment of forest species (Parrotta *et al.* 1997). Fluctuations in temperature and soil humidity are reduced under such trees (Belsky *et al.* 1989), whereas soil fertility may be improved by decomposition of falling leaves and animal excretions (Belsky *et al.* 1989, Kellman 1979, Puerto & Rico 1988, Radwanski & Wickans 1967, Weltzin & Coughenour 1990). Soil water capacity could increase as well (Joffre & Rambal 1988). Facilitation of establishment of late-successional woody plants could explain the higher rate of plant biomass production beneath remnant trees. In contrast, light conditions in open fields are unfavourable to germination and seedling growth of many forest species (Guevara *et al.* 1992), favouring instead strict large-gap and light-demanding pioneer species (e.g. *M. cecropioides* in this study) and light-demanding herbs. This is reflected in our study by the significant decrease of BA of clonally growing large herbs with age of fallow beneath remnant trees. Different pioneer species have different requirements and ecological properties, and vary in their contribution to forest regrowth because they colonise at different stages of regeneration (Finegan 1996). Thus later-arriving pioneer species (with lower light requirements) could establish more rapidly beneath remnant trees, thereby short-cutting the first stage of succession. We observed *Musanga cecropioides* (a typical gap species arriving very early in succession) more frequently away from the crowns of remnant trees than beneath them, whereas some later-stage pioneer species (e.g. *Ficus* spp., *Myrianthus arboreus*, *Macaranga hurifolia*) were observed almost exclusively under the crowns of remnant trees. However, some studies have shown that most species (pioneers as well as forest species) present a complex growth response, in which they resemble the shade-intolerant extreme in some aspects of the response, and the shade-tolerant extreme in other aspects (Popma & Bongers 1988). Such species grow rapidly under high-light conditions, but also tolerate low light levels, under which conditions they grow much more slowly. We can imagine that species found under the crowns of the trees are not strict light-demanding pioneers, but species that are shade-tolerant in some stages of their development.

Absence of marked effect of the species identity of remnant trees

Species effects on the variables analysed were quite unpredictable and presented a wide range of responses, depending on the factors and variable considered. More light-demanding clonally propagating herbs occurred away from the crown of *T. scleroxylon* than beneath, while no such effect was seen for *P. angolensis*. This difference could be due to the denser shade beneath *T. scleroxylon* than beneath *P. angolensis*. Our study suggests that the effects of species of remnant tree on the structure and composition of regrowth beneath them are complex, including effects on seed rain (Carrière *et al.* 2002) and on abiotic conditions beneath the trees.

Guevara *et al.* (1986) and Slocum (1997) showed that seed rain was higher beneath remnant trees that produce fleshy fruits; Guevara *et al.* (1992) found that species richness of regrowth was higher beneath zoochorous remnant trees than beneath those with other dispersal modes. Similarly, Vieira *et al.* (1994) emphasized the role of fleshy fruits of *Cordia multispicata* as a magnet for seed-dispersing frugivores. We thus initially predicted that regenerating vegetation would be more diverse beneath *Pycnanthus*, based on the further prediction that seed rain beneath this tree, which provides fleshy fruits eaten by a large number of bird and mammal species, would be greater and more diverse than that beneath *Triplochiton*, whose seeds are wind-dispersed. This last prediction was not upheld; indeed, seed rain was significantly more abundant and diverse beneath *Triplochiton* (Carrière *et al.* 2002). It is thus perhaps not surprising that our first prediction was also rejected, and that BA and number of stems of regenerating vegetation accounted for by seedlings beneath remnant *Triplochiton* both tended to be greater than beneath *Pycnanthus*. Dispersal mode of the remnant tree is only one of many factors affecting species richness or total biomass production of regrowth beneath them. Wind-dispersed tree species might possess other characteristics attractive to animals, such as dense foliage or high crowns. In our site, wind-dispersed trees are mostly large emergents. On the other hand, factors such as the distribution and habitat characteristics of neighbouring forests may be important in influencing composition and changes in structure and biomass during the latter stages of secondary regrowth.

Low correspondence between composition of seed rain and regeneration beneath trees

Endozoochorous seeds accounted for the majority of seed rain (94.5%, Carrière *et al.* 2002) and of individual stems in regeneration, and dominance of both endozoochorous seeds and stems originating from them was greater beneath remnant trees than away from their crowns. Although the large number of undetermined species in the seed rain makes it difficult to compare at the species level the results reported here with the composition of seed rain (Carrière *et al.* 2002), it is clear that, except for *Musanga* (which dominated seed rain and was well represented in regeneration) there was little correlation between species abundances in our samples of seed rain and regenerating vegetation. For example, of the nine most common tree species in regeneration, only four were even represented in the seed rain (see Results section). Similarly, more common species represented in seed rain were not present in regenerating vegetation. This points to the importance of differences in establishment success in determining composition of regenerating vegetation. Remnant trees appear to be a major factor influencing conditions for establishment in the system studied here.

Effect of age of fallow beneath remnant trees

BA of regenerating vegetation increased rapidly with age of fallow beneath remnant trees, but very slowly away from their crowns (Figure 5). Differences in BA among quadrats beneath remnant trees remained non-significant, because of the large variations and high standard deviations in BA among quadrats. These differences and variations apparently developed between 5 and 10 y after abandonment of cultivation. This period may correspond to a critical phase of competition or other processes (such as predation) that condition seedling establishment or sapling growth. Studies in Amazonia have shown that the variability in biomass accumulation in fallows of different ages was greatest among 12–15-y-old stands and appeared to be dependent on the timing of canopy recruitment of later-successional trees in relation to the senescence of large pioneers (Steininger 2000). Whatever factors are responsible, young secondary forest located under the crowns of standing trees already presents some characteristics of older secondary regrowth, with relatively tall trees and a sparse, shaded undergrowth (S. Carrière, *pers. obs.*). This means that relatively mature forest stages could be reached sooner than in fallows without remnant trees. Moreover, the presence of scattered large trees creates a more heterogeneous landscape in which various stages of secondary regrowth coexist in the same field, increasing biodiversity at both field and agrosystem levels.

We have shown that remnant trees play a considerable role in several aspects of forest regeneration. Despite the explanatory power of the variables we have focused on, substantial residual variation among fields remains unexplained.

Differential effects of different tree species on soil conditions could be very important (Sirois *et al.* 1998). Management or land-use history of the field could be the most important factor that could lead to differences in composition and structure of regrowth (Guevara *et al.* 1992, Uhl 1987) and biomass accumulation (Steininger 2000). Type of forest vegetation that was cleared, degree of completeness of burning after field clearing, the number of times the field was cultivated since it was first cleared, and finally the underlying environmental heterogeneity (e.g. edaphic differences) independent of human disturbance, could combine to increase the variation in composition and structure observed in regeneration.

Increased number and faster growth of woody plants beneath remnant trees should result in more rapid transition to mature forest. By their growth, newly recruited trees would expand these 'nuclei', which eventually coalesce (Yarranton & Morrison 1974). Remnant trees could thus contribute to (1) optimize the fallow period, which is closely related to the above-ground woody vegetation and biomass accumulation for the next cycle of slashing and burning; and (2) create new continuous forest patches where cultivation is indefinitely abandoned, or where cocoa agroforestry plantations are adopted (Carrière 1999). This kind of agroforestry system accounts for a large part of forested areas around most villages in Central Africa. Complex multi-storey cocoa plantations provide both non-timber forest products and a cash crop (Carrière 1999, Dounias 1996). To a certain extent they also maintain plant and animal biodiversity at higher levels than found in many other agroecosystems (MacDonald 1982).

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