Capítulo 3

Three types of seedling establishments of tree species in an amazonian terra-firme forest

Três tipos de estabelecimento de mudas de espécies arbóreas em uma floresta de terra-firme amazônica

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SUMMARY: We studied the characteristics of seedling establishment of several tree species in an Amazonian terra-firme forest. We counted the seedlings (less than 1.5 m high), identified their species and measured their height in 52 fixed-area plots (4 m long and 1m wide each) that were established randomly under closed canopies (26 plots) and in gaps (26 plots). For each species, we calculated the mean density of the seedlings (Ds), the ratio of the number of plots in which the species appeared (Rq) and the concentration indices that showed the percent of seedlings concentrated in one plot (C1) or two plots (C2). Altogether, there were 3,805 seedlings in 52 plots. *Duguetia flagellaris* Huber., *Protium apiculatum* Swartz and *Palicourea anisolaba* M. Arg. showed high Ds and large Rq under both the closed canopies and in the gaps. *Goupia glabra* Aubl. and *Vismia guianensis* (Aubl.) Choisy showed higher Ds and larger Rq in the gaps than those under the closed canopies. *Hemicrepidospermum rhoifolium* (Bth.) Swart., *Swartzia ulei* Harms. and *Sclerolobium setiferum* Ducke showed a large concentration index (C1 or C2) under the closed canopies. While *Sloanea guianensis* (Aubl.) Bth. and *P. apiculatum* showed a large concentration index (C1 or C2) in the gaps. Three types of seedling establishments were extracted. In the first type, the gap-demanding type, seedlings were established only in the gaps (e.g. *G. glabra*). In the second type, the concentrated-germination type, seedlings were concentrated around the mother trees (e.g. *S. guianensis*). In the third type, the unrestricted-germination type, seedlings were found everywhere on the forest floor (e.g. *P. apiculatum*). These results should be useful for understanding the strategies of

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regeneration of tree species in Amazonian terra-firme forest.
Key-words: gap, regeneration, seedlings, terra-firme forest

RESUMO: As características de estabelecimento de mudas de várias espécies arbóreas da floresta de terra-firme foram estudadas na região de Manaus. Foram consideradas mudas, indivíduos com altura total menor que 1,5 m. Em 52 amostras de 4 por 1 m cada, todas as mudas foram identificadas e medidas. As amostras foram distribuídas aleatoriamente na área de estudo, sendo 26 em áreas de floresta fechada e 26 em areas de clareiras. Para cada espécie, foi determinada a densidade media das mudas (Ds), a razão do número de amostras nas quais aparecem a espécie (Rq) e os índices de concentração que mostram a percentagem das mudas concentradas em uma amostra (C1) ou em duas amostras (C2). Na área total amostrada foram encontradas 3.805 mudas. *Duguetia flagellaris* Huber., *Protium apiculatum* Swartz e *Palicourea anisolaba* M. Arg. apresentaram altos Ds e Rq tanto em floresta fechada como em clareiras. *Goupia glabra* Aubl. e *Vismia guianensis* (Aubl.) Choisy apresentaram maiores Ds e Rq em clareiras do que na floresta fechada. *Hemicrepidospermum rhoifolium* (Bth.) Swart., *Swartzia ulei* Harms. e *Sclerolobium setiferum* Ducke apresentaram um alto índice de concentração (C1 e C2) em floresta fechada, enquanto que, *Sloanea guianensis* (Aubl.) Bth. e *P. apiculatum* apresentaram altos índices em clareiras. Foram identificados três tipos de estabelecimento de mudas: (1) espécies de clareira, espécies que se estabelecem apenas em clareiras (e.g. *G. glabra*); (2) espécies que se estabelecem em torno da árvore-mãe (e.g. *S. guianensis*) e (3) espécies irrestritas, mudas germinadas aleatoriamente no chão da floresta (e.g. *P. apiculatum*). Esses resultados podem ser úteis no entendimento das estratégias de estabelecimento, usadas pelas espécies arbóreas de florestas de terra-firme da Amazônia.
Palavras-chave: clareira, regeneração natural, mudas florestais.

INTRODUCTION

In the tropical forest, the environmental condition differs entirely with the site, such as light environment (e.g. Chazdon 1988, Whitmore et al. 1993, Montgomery and Chazdon 2002) and soil conditions (e.g.Vitousek and Denslow 1986, Ferraz et al. 1998). In various environments of tropical forests, there are large numbers of tree species (Gentry 1990, Prance 1990). Many tree species have evolved their strategies of regeneration, through inter-specific competition, to match their environments. This variability in the strategies of regeneration enables tremendous tree species to coexist in the tropical forests (Whitmore 1984).

Recently, the deforestation and devastation, caused by the regional development through different land uses have become serious problems in the Amazon region. A tremendous area of tropical forest is disappearing year by year. Approximately 600,000 km2 of forest area had already disappeared up to 2000 in the Amazon (INPE, 2001). Therefore, reforestation and rehabilitation of deforested land are urgently necessary in the Amazon region. For this, the variability of the regeneration of many tree species should be taken into consideration. It is necessary that we understand the characteristics of regeneration of various tree species in the Amazonian natural forests.

To understand the characteristics of the regeneration of trees, it is helpful to separate the life history of the trees into several growing stages. Niiyama and Abe (2002) analyzed the demography of trees throughout the life cycle by a matrix model with 7 growing stages. Early stages of life history, especially the seedling stage, are the most important stages to survive throughout its life (Whitmore 1996). The number of individuals decreases drastically in the seedling stage (Alvarez-Buylla and Martinez-Ramos 1992). In the matrix model proposed by

Niiyama and Abe (2002), the transition probability from seed or seedling to sapling stage (height > 30 cm) was much lower than that from sapling to later stages. Therefore, the study on seedling establishment will provide important information for understanding the characteristics of the regeneration of the species. In the present study, we focused on the seedling establishment to understand a characteristic of regeneration. Since the species in different ecological guilds present different niche preferences for seed germination (Vieira 1992), there would be various patterns of seedling establishment. The aim of the present study is to extract each type of seedling establishment and to classify the tree species in the Amazonian terra-firme forest into the patterns.

METHODS

The study site is at the ZF-2 Experimental Station of the National Institute for Research in the Amazon (INPA) located approximately 60 km northwest of Manaus, AM, Brazil. It is the Amazonian terra-firme forest (Vieira, 1992 and Silva et al., 2002). To study the characteristics of seedling establishment, 52 quadrates were set up along the two belt-transects (20 m wide and 2,500 m long) that had been established to study the structure and floristic composition of the site in the Brazilian Amazon Forest Research Project Phase I, JICA-INPA (c.f. Higuchi *et al.*, 1998 and Ferraz *et al.*, 1998). Each quadrate was 1 m wide and 4 m long (4 m^2 in area). Twenty-six quadrates were located randomly under the closed canopies and the others were located randomly in the canopy gaps. All seedlings of trees in the quadrates were tagged with the ravel, their local names identified and their height measured. In the present study, seedlings were defined as individuals less than 150 cm in height. In the analysis, the scientific name of the tree was determined from the local name with reference to Higuchi *et al.* (1985), Jardim and Hosokawa (1986-87), Ribeiro et al. (1999) and Silva et al. (2002). We selected twelve species that showed a distinctive appearance for analysis (Table 1). We calculated the mean of the seedling density (Ds; seedlings per a quadrate (4 m^2)), its standard deviation (S.D.) and the ratio of the number of the quadrate that the species appeared (Rq; %) for each plant species by the following equations:

$$Ds = \Sigma D_i / N_{tot}$$

$$S.D. = (\Sigma (Ds - D_i)^2 / N_{tot})^{0.5}$$

$$Rq = Nq / N_{tot}$$

where D_i is the seedling density of each quadrate, N_{tot} is the total number of quadrates and Nq is the number of the quadrates in which the seedlings of the species appeared.

We also calculated the concentration indices that showed the percent of the seedlings concentrated to one quadrate (C1; %) or two quadrates (C2; %) for each species by the following equations:

$$C1 = n_{max1} / n_{tot}$$

$$C2 = (n_{max1} + n_{max2}) / n_{tot}$$

where n_{max1} and n_{max2} are the largest and second largest number of seedlings of a given species in a quadrate respectively, and n_{tot} is the total number of the seedlings of the species.

RESULTS

In total, 3,805 seedlings with 194 local names appeared in 52 quadrates (208 m^2 in area). Table 2 shows the Ds ± S.D. of 12 species under the closed canopy and in the gaps. The mean Ds of all species ("Total" in Table 2) under the closed canopies (0.36 seedlings/4m^2/species) was not

Table 1 - List of the species analysed in the present study.

Spesies	Family	Local name
Duguetia flagellaris Huber.	Annonaceae	Envira amarela
Hemicrepidospermum rhoifolium (Bth.) Swart.	Burseraceae	Breu Branco
Protium apiculatum Swartz	Burseraceae	Breu vermelho
Swartzia ulei Harms.	Caesalpiniodeae[1)]	Muirajiboia jerimum
Sclerolobium setiferum Ducke	Caesalpiniodeae[1)]	Tachi vermelho
Goupia glabra Aubl.	Celastraceae	Cupiuba
Tapura amazonica Poepp. & Endl.	Dichapetalaceae	Tapura
Sloanea guianensis (Aubl.) Bth.	Elaeocarpaceae	Urucurana
Vismia guianensis (Aubl.) Choisy	Guttiferae	Lacre vermelho
Symphonia globulifera Linn.	Guttiferae	Anani
Miconia elaeagnoides Cogn.	Melastomataceae	Buxixu canela de velho
Palicourea anisolaba M. Arg.	Rubiaceae	Taboquinha

1): Caesalpiniodeae is a subfamily of the Leguminosae

Table 2 - The mean seedling density and its standard deviation (S.D.) for each species.

Species	Seedling Density ± S.D. (seedlings / 4m²) Closed canopies		Gaps		p value
D. flagellaris	4,88 ± 8,12	*h*	2,00 ± 3,02	*h*	0,0991
H. rhoifolium	7,23 ± 24,67	*h*	0,15 ± 0,37		0,1561
P. apiculatum	5,77 ± 16,07	*h*	27,85 ± 108,78	*h*	0,3154
S. ulei	2,88 ± 13,90	*h*	0,19 ± 0,49		0,3330
S. setiferum	3,00 ± 12,95	*h*	0,38 ± 0,75		0,3137
G. glabra	0,04 ± 0,20	*l*	0,77 ± 1,18		0,0044
T. amazonica	1,23 ± 1,75	*h*	2,31 ± 4,42	*h*	0,2560
S. guianensis	0,08 ± 0,27		4,58 ± 16,06	*h*	0,1655
V. guianensis	0,04 ± 0,20	*l*	0,81 ± 1,39		0,0095
S. globulifera	0,12 ± 0,59		1,12 ± 5,49	*h*	0,3640
M. elaeagnoides	0,23 ± 0,59		1,00 ± 1,83	*h*	0,0505
P. anisolaba	2,50 ± 2,64	*h*	3,23 ± 3,18	*h*	0,3718
Others	0,23 ± 0,29		0,18 ± 0,08		0,3850
Total	0,36 ± 0,29		0,39 ± 0,54		0,7694

Others and Total show the average of the other species and all species respectively. Alphabets indicate significant difference (*h* : higher, *l* : lower) from the Total by Fisher's exact probability test ($p<0.05$). The value of "p" indicates the significance of the difference of the value under the closed canopies with that in the gaps by Welch's t-test.

significantly different from that in the gaps (0.39 seedlings/4m^2/species). *Duguetia flagellaris* Huber., *Protium apiculatum* Swartz, *Tapura amazonica* Poepp. & Endl. and *Palicourea anisolaba* M. Arg. showed significantly higher seedling density than the "Total" both under the closed canopies and in the gaps ($p < 0.05$ by Fisher's exact probability test, Table 2). *Hemicrepidospermum rhoifolium* (Bth.) Swart., *Swartzia ulei* Harms. and *Sclerolobium setiferum* Ducke showed high seedling density only under the closed canopies. *Goupia glabra* Aubl. and *Vismia guianensis* (Aubl.) Choisy showed significantly higher seedling density in the gaps than under the closed canopies ($p < 0.05$ by Welch's t-test). *Miconia elaeagnoides* Cogn. also showed a higher seedling density in the gaps in contrast to that under the closed canopies ($p=0.05$). *Duguetia flagellaris, P. apiculatum* and *P. anisolaba* showed significantly larger Rq than the "Total" both under the closed canopies and in the gaps, too ($p<0.05$ by Fisher's exact probability test, Table 3). *Goupia glabra* and *V. guianensis* showed significantly larger Rq in the gaps than under the closed canopies. *Hemicrepidospermum rhoifolium*, *S. ulei* and *S. setiferum* showed significantly larger concentration index (C1 or C2) than the "Total" under the closed canopies ($p < 0.05$ by Fisher's exact probability test, Table 4). On the contrary, *P. apiculatum* and *Sloanea guianensis* (Aubl.) Bth. showed significantly larger concentration index in the gaps (Table 4). *Symphonia globulifera* Linn. also showed large concentration indices in the gaps although there were no significant differences ($p = 0.071$ for C1, $p = 0.284$ for C2) because of the small number of seedlings ($n = 29$, Table 4). Most seedlings of all species were less than 40 cm in height (Fig. 1 and Fig. 2). However, *D. flagellaris*, *P. apiculatum*, *T.*

Table 3 - The ratio of the number of quadrates in which the species appeared (Rq).

Specie	Rq		p-value
	Closed canopies	Gaps	
D. flagellaris	61,5% *l*	61,5% *l*	> 0.99
H. rhoifolium	23,1%	15,4%	0,733
P. apiculatum	57,7% *l*	80,8% *l*	0,517
S. ulei	19,2%	15,4%	> 0.99
S. setiferum	19,2%	26,9%	0,752
G. glabra	3,8%	38,5%	0,017
T. amazonica	50,0% *l*	42,3%	0,808
S. guianensis	7,7%	15,4%	0,671
V. guianensis	3,8%	38,5%	0,017
S. globulifera	3,8%	7,7%	> 0.99
M. elaeagnoides	15,4%	34,6%	0,351
P. anisolaba	84,6% *l*	80,8% *l*	> 0.99
Others	8,4%	8,4%	> 0.99
Total	9,7%	10,3%	> 0.99

Others and Total show the average of the other species and all species, respectively. Species with alphabet *l* show significantly larger Rq than that of the Total by Fisher's exact probability test ($p<0.05$). The value of "p" indicates significance of the difference of the value under the closed canopies with that in

Table 4 - The total number of seedlings (n) and the concentration indices (C1 and C2).

Species	Concentration indices					
	Closed canopies			Gaps		
	n	C1	C2	n	C1	C2
D. flagellaris	127	27,6% *s*	44,1% *s*	52	19,23% *s*	38,5% *s*
H. rhoifolium	188	53,2%	96,3% *l*	4	-	-
P. apiculatum	150	50,7%	75,3%	724	76,80% *l*	85,2% *l*
S. ulei	75	94,7% *l*	96,0%	5	-	-
S. setiferum	78	84,6% *l*	94,9%	10	30,0%	50,0%
G. glabra	1	-	-	20	20,00%	35,0%
T. amazonica	32	18,8% *s*	34,4% *s*	60	25,00% *s*	50,0%
S. guianensis	2	-	-	119	56,30%	98,3% *l*
V. guianensis	1	-	-	21	23,81%	42,9%
S. globulifera	3	-	-	29	96,55%	100,0%
M. elaeagnoides	6	-	-	26	26,92%	46,2%
P. anisolaba	65	20,0% *s*	30,8% *s*	84	14,29% *s*	26,2% *s*
Others	1085	54,7%	76,2%	838	54,65%	71,2%
Total	1813	53,4%	75,3%	1992	58,63%	73,8%

Others and Total show the average of the other species and all species, respectively. Alphabets indicate significant difference (*l* : larger, *s* : smaller) from the Total by Fisher's exact probability test ($p<0.05$).

amazonica and *P. anisolaba* had relatively many seedlings even in the height classes below 40 cm (Fig. 1 and Fig. 2).

DISCUSSION

Based on the present results, we extracted three types of seedling establishments strategy from the various patterns of seedling appearance (Table 5). The first is the gap-demanding type. The seedling establishment of this type is restricted to the gaps. Seeds of this type germinate only in the gaps. This type contains pioneer species. Seedlings of this type show high Ds in the gaps and low Ds under closed canopies. Seeds of the pioneer species are dispersed widely by animals or by wind (Howe, 1986 and Alvarez-Buylla and Martinez-Ramos, 1990) and wait to germinate as buried seeds until gaps are formed (Garwood, 1989, Masaki et al., 1998 and Iida and Masaki, 2002). The longevity of the seed is reportedly longer in pioneer species than in shade-tolerant species in Amazonian terra-firme forest (Vieira 1992). Therefore, Rq will become relatively large in the gaps; *G. glabra*, *V. guianensis* and *M. elaeagnoides* belong to this type.

The second type is the concentrated-germination type. Species of this type establish seedlings concentrated in a small area. However, few seedlings are found except in a concentrated area. The concentrated area is considered to be around the mother tree. There were conspecific trees that were considered as mother trees, near the quadrates where seedlings of a species were concentrated in the present study. The seedling establishment of this type may be restricted to around the mother trees rather than to the gaps. This type shows a small Rq both under the closed canopies and in the gaps and a large concentration index under the closed

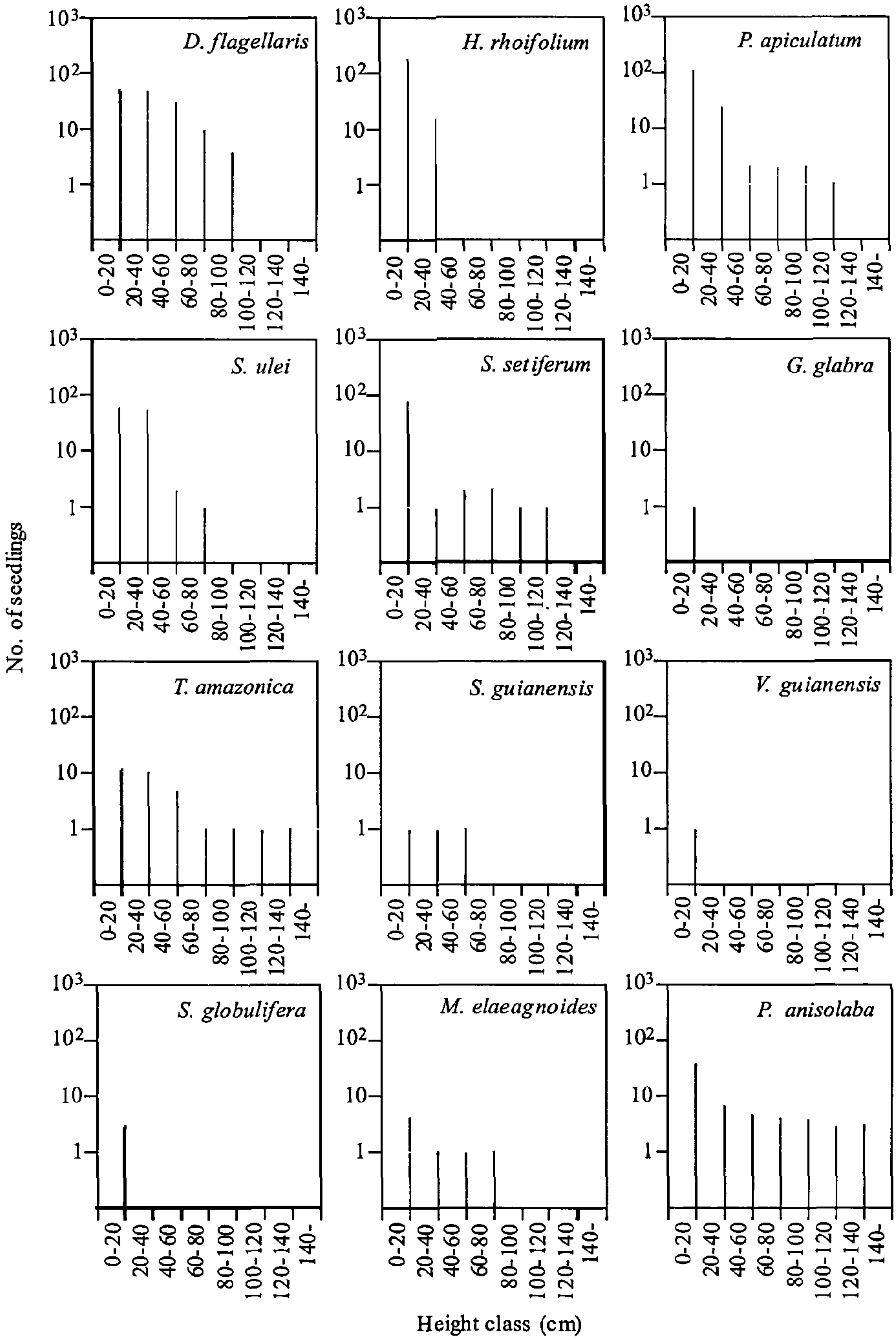

Figure 1 - The distribution of seedling size (height) under the closed canopies.

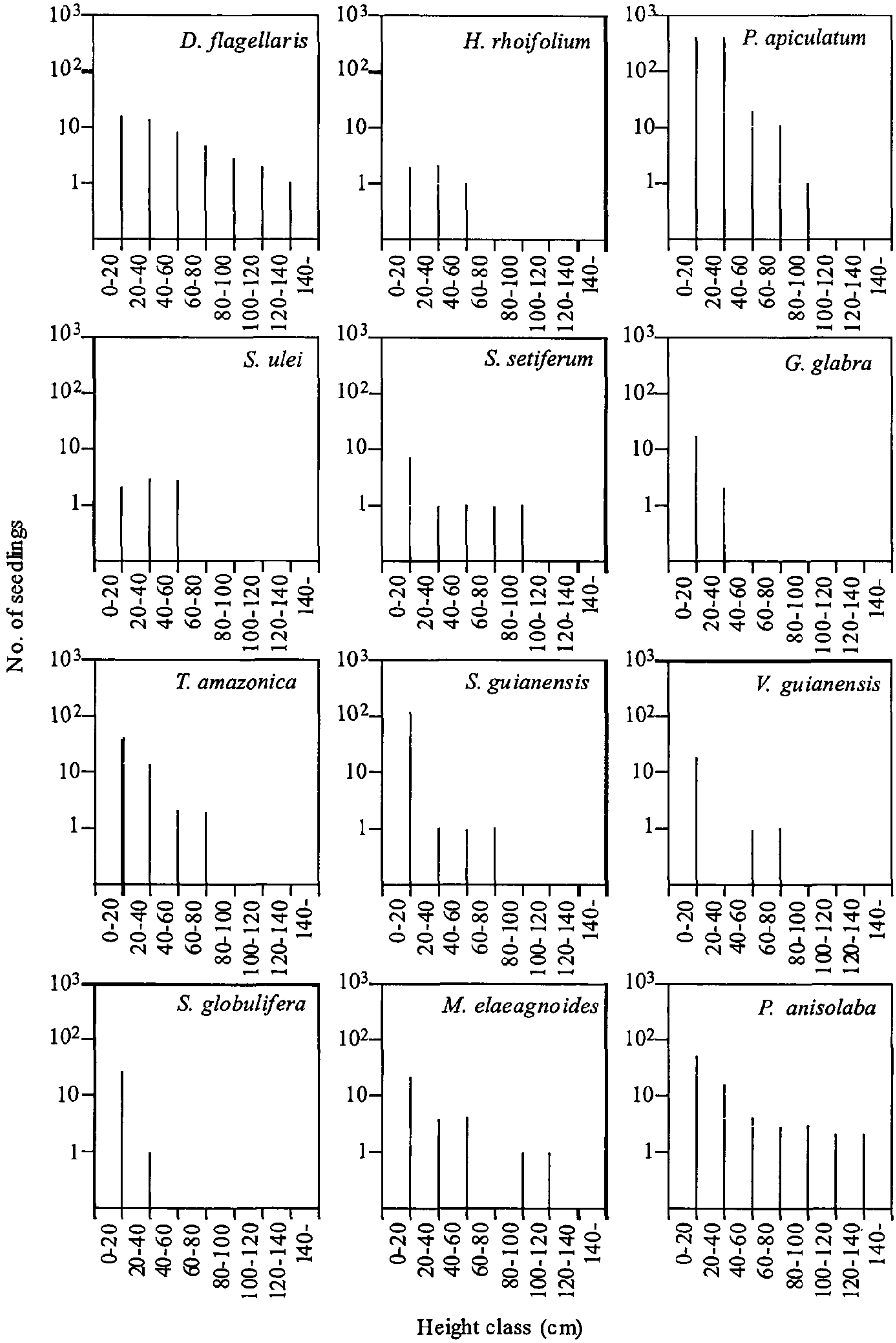

Figure 2 - The distribution of seedling size (height) in the gaps.

Table 5 - Classification of the characteristics of the seedling establishment in terra-firme forest in Central Amazon.

Type	Seedling density		Rq		Concentration indices		Species
	Closed	Gaps	Closed	Gaps	Closed	Gaps	
Gap-demanding type	low	high	-	relatively large	-		*G. glabra*, *V. guianensis*, *M. elaeagnoides*
Concentrated-germination type	high in the Closed or Gaps		small	small	high in the Closed or Gaps		*H. rhoifolium*, *S. ulei*, *S. setiferum*, *S. guianensis*, *S. globulifera*
Unrestricted-germination type	high	high	large	large	generally small		*D. flagellaris*, *P. apiculatum*, *T. amazonica*, *P. anisolaba*

canopies or in the gaps. *Hemicrepidospermum rhoifolium*, *S. ulei* and *S. setiferum* belong to this type. *Sloanea guianensis* and *S. globulifera* that had high Ds in the gaps are also considered to belong to this type rather than to the gap-demanding type because of the low Rq in the gaps.

The third one is the unrestricted-germination type. Seedlings of this type are found everywhere on the forest floor. They are able to germinate even under the closed canopies. They show high Ds and large Rq both under the closed canopies and in the gaps. *Duguetia flagellaris*, *T. amazonica* and *P. anisolaba* belong to this type. *Protium apiculatum* is also considered to belong to this type because of the large Rq both under the closed canopies and in the gaps although it showed a large concentration index. Species of this type might have shade-tolerant characteristics. The size distribution of the seedlings shown in Fig. 1 and Fig. 2 suggests that seedlings of this type would survive and to grow consistently even under closed canopies.

Swaine and Whitmore (1988) dichotomized the guild of regeneration, pioneer and climax, and many studies have been developed based on their work (e.g. Oldeman and Dijik 1991, Finegan 1992, Yamamoto 1992). The gap-demanding type and unrestricted-germination type in the present study may be the pioneer and climax species according to Swaine and Whitmore (1988), respectively. Alvarez-Buylla and Martinez-Ramos (1992) pointed out that the pioneer-climax framework represented the extremes of a continuum of characteristics of regeneration. The indication made by Alvarez-Buylla and Martinez-Ramos (1992) might apply to the present classification. The three types found in our study (Table 5) would be the extremes of a continuous pattern of seedling establishment. *Protium apiculatum* that was classified into the unrestricted-germination type in the present study also had the characteristics of both the gap-demanding type (high Ds in the gaps, Table 2) and the concentrated-germination type (large concentration index, Table 4). However, classifying tremendous species into some guilds of regeneration would be helpful to understand their property (Whitmore 1996, Yamamoto 1992, Saito *et al.* 2002). The present study showed one of the important information of the regeneration, especially early stages of the life cycle. Regeneration of trees should be considered from various aspects: seed production, growth rate (Silva et al., 2002), survival rate or mortality of individuals and site preferences. Further studies are necessary to evaluate the regeneration characteristics of trees in Amazonian terra-firme forests. These studies will construct a base of the theory for the reforestation or rehabilitation of the degraded areas in the Amazon.

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