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Forest dynamics in flood plain forests in the Peruvian Amazon: effects of disturbance and implications for management

Gustav Nebel[a,*], Lars Peter Kvist[a], Jerome K. Vanclay[b], Héctor Vidaurre[c]

[a]Department of Economics and Natural Resources, Unit of Forestry, The Royal Veterinary and Agricultural University, Rolighedsvej 23, 1958 Frederiksberg C, Denmark
[b]School of Resource Science and Management, Southern Cross University, P.O. Box 157, Lismore NSW 2480, Australia
[c]Instituto de Investigaciones de la Amazonia Peruana, Av. Abelardo Quiñones Km. 2.5, Iquitos, Peru

Abstract

Forest dynamics were studied from 1993 to 1997 for individuals ≥10 cm DBH in nine 1 ha permanent sample plots. They were established in natural flood plain forests located on the lower Ucayali river in the Peruvian Amazon. After inventories of three plots in each of three forest types, a light and a heavy felling treatment were applied to each of the two plots, while a third plot was kept untreated. Average annual stem mortality and recruitment rates in the untreated plots were among the highest observed in neotropical rain forests: mortality 2.2–3.2% per year, recruitment 3.0–4.6% per year. Dead individuals deviated significantly from random dispersion towards clumping. The average annual basal area growth was around 1 m^2/ha per year, corresponding to average annual basal area growth rates of 3.5–3.8% per year in the untreated plots. No decrease in basal area growth was observed even in the treated plots where annual basal area mortality rates up to 41% during the first year were observed. The average diameter growth increased from 4.0–4.5 mm per year in the untreated plots to 5.3–6.8 mm per year in the treated plots. The stocking of commercial timber species was high with basal areas of 2.6–10.0 m^2/ha and volumes of 59–240 m^3/ha. The corresponding growth of basal area and volume of commercial timber species were also considerable, reaching values of 0.1–0.3 m^2/ha per year and 2–9 m^3/ha per year, respectively. These attributes suggested that forest management for timber production in these forests can be flexible and provide relatively high yields on a sustained basis. It appeared that management interventions can be carried out within the range of naturally occurring perturbations, although it should be noticed that only limited proportions of each habitat are disturbed at a time by nature. The patchy occurrence of habitats may provide logistic problems to management.

Keywords: Wetlands; Mortality; Recruitment; Growth; Forest succession; Silviculture; Permanent sample plots

1. Introduction

Sustainable use and management of natural tropical rain forests remain topical issues and pose interesting problems relating to cultural, socio-economic and political conditions (e.g. Buschbacher, 1990; Vanclay, 1993; Bruenig, 1996). However, it is clear that sustainable use and management of the tropical rain forests requires better knowledge on how these ecosystems function and respond to management interventions (e.g. Gómez-Pompa and Burley, 1991; Hubbell, 1995; Whitmore, 1995), despite recent advances (e.g. Leigh et al., 1982; Graff, 1986; Lamprecht, 1989, 1993; Silva, 1989; Bawa and Hadley, 1990; Gómez-Pompa et al., 1991; McDade et al., 1994; Vanclay, 1994; Richards, 1996).

* Corresponding author. Tel.: +45-35-28-22-32;
fax: +45-35-28-26-71.
E-mail address: gne@kvl.dk (G. Nebel).

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The present paper provides information on forest dynamics of natural and disturbed flood plain forests in the Peruvian Amazon. These forests are among the most intensively used in the area, and provide a wide range of products for commercial and subsistence purposes (e.g. Kvist et al., 1995, 2001a,b; Kvist and Nebel, 2001), which highlights the need for a better understanding of the way they function and respond to interventions. Notwithstanding this to date there have been few reports on growth and dynamics of Amazonian flood plain forests obtained from remeasurement of permanent sample plots (Gentry and Terborgh, 1990; Korning and Balslev, 1994a). Forest dynamics processes were therefore studied for individuals $\geq$10 cm diameter at breast height (DBH) in nine 1 ha permanent sample plots over a 4-year period following felling treatments in some of the plots. Mortality, recruitment and growth were analysed and compared to other studies, and forest succession patterns were described. Finally, implications for forest management and conservation were discussed.

2. Study area

Amazonian high restinga, low restinga, and tahuampa flood plain forests were studied approximately 10 km south-west of Jenaro Herrera (4°55′S, 73°44′W) in the Peruvian Loreto Department. General aspects of Peruvian flood plain forests were described by Kvist and Nebel (2001). The location, the growth conditions, and the floristic composition and structure of the overstorey (individuals $\geq$10 cm DBH) in the forests studied were described by Nebel et al. (2001a). Similarly, the understorey (trees 1.5 m high to 10 cm DBH) floristic composition and structure in restinga forests were described and compared to the overstorey by Nebel et al. (2001b).

3. Methods

From July to November 1993 nine 1 ha permanent sample plots were established with three plots located in each of three forest types: plots 1–3 in high restinga, plots 4–6 in low restinga, and plots 7–9 in tahuampa. All individuals $\geq$8.5 cm DBH were permanently marked and relevant measurements were carried out (Nebel et al., 2001a) so that growth data would be available for all individuals $\geq$10 cm DBH. Directional felling of selected trees was carried out to investigate the response of the forests to disturbance. Felling in the high and low restinga forests took place in December 1993 and January 1994, respectively. Due to early flooding the tahuampa forest was not treated until August 1994. In each forest type one plot was left untouched (plots 3, 6, and 9), while the remaining two plots were treated with a moderate (plots 2, 5, and 8) and a heavy felling (plots 1, 4, and 7), respectively. The felled trees were scattered over the plots, and left on the felling site to decay. A 20 m wide zone surrounding all the treated plots was established and treated with the same felling intensities as inside the plots. In plots where a heavy treatment was carried out, one tree was felled in each 20 m $\times$ 20 m quadrant of the plots (18–26% of the basal area), while for the moderate treatment one tree in every alternate 20 m $\times$ 20 m quadrant was cut (6–11% of the basal area; Table 1).

The plots were remeasured during August–September 1994, September–November 1995, and August–October 1997, including registration of dead individuals and assessment of crown position and form according to Dawkins classification (Alder and Synnott, 1992). In 1994, the DBH of all but the largest trees was remeasured at marked measurement points. Because some measurements were missed in 1994 these data were not used in calculating basal area

Table 1
Felling treatments carried out in permanent sample plots located in flood plain forests at Braga–Supay and Lobillo

	Plot					
	1	2	4	5	7	8
Forest type	High restinga	High restinga	Low restinga	Low restinga	Tahuampa	Tahuampa
Treatment	Heavy	Moderate	Heavy	Moderate	Heavy	Moderate
Stems felled (% of total)	25 (5.3)	13 (2.9)	29 (5.5)	15 (2.5)	25 (4.8)	13 (2.6)
Basal area felled (% of total)	6.40 (25.5)	2.69 (10.8)	3.66 (18.4)	1.50 (6.3)	5.51 (20.3)	2.94 (10.2)

growth of surviving trees and DBH increment. In 1995 and 1997, the DBH was also measured at marked measurement points, and ingrowth of new individuals exceeding 8.5 cm DBH was recorded following the method used during plot establishment (Nebel et al., 2001a).

Rates of mortality, recruitment, and basal area growth were calculated using a model for exponential growth in continuous time (e.g. Begon et al., 1996; Hastings, 1996; Kimmins, 1997). The annual mortality rates were calculated as follows (e.g. Lieberman et al., 1985a; Phillips et al., 1994; Condit et al., 1995):

$$r_{\mathrm{m}} = \frac{\ln(N_0) - \ln(N_0 - N_{\mathrm{m}})}{\Delta t}$$

and annual recruitment rates as (Phillips et al., 1994):

$$r_{\mathrm{r}} = \frac{\ln(N_0 - N_{\mathrm{m}} - N_{\mathrm{r}}) - \ln(N_0 - N_{\mathrm{m}})}{\Delta t}$$

and annual basal area growth rates as:

$$r_{\mathrm{g}} = \frac{\ln(N_0 - N_{\mathrm{m}} + \Delta N) - \ln(N_0 - N_{\mathrm{m}})}{\Delta t}$$

where N_0 is the stem number or the basal area at the beginning of the period Δt; N_{m} and N_{r} are the individuals or the basal area that died or was recruited during the period Δt, respectively; ΔN is the basal area increment of individuals surviving the period Δt. The stand half-life and the stand doubling time (T) of the initial population were calculated from the annual rates of stem mortality and stem recruitment (r), respectively:

$$T = \frac{\ln(2)}{r}$$

The dispersion patterns of dead individuals $\geq$10 cm DBH in the untreated plots were evaluated using the Morisita index of dispersion (I_δ) calculated for varying plot quadrat sizes (side lengths 5, 10 and 20 m, respectively):

$$I_\delta = \frac{\sum_{i=1}^{q} n_i(n_i - 1)}{N(N-1)} q$$

where $n_1, \ldots, n_q$ are the numbers of individuals observed in each of q quadrats and N is the total number of individuals observed. The departure from randomness ($I_\delta = 1.0$) was tested by means of an F-test (Greig-Smith, 1983).

For commercial species several stand and growth parameters were evaluated. All species indicated as commercially valuable in interviews with local people (Kvist et al., 2001a) were included in the analyses. In calculations of volumes a form factor for total stem and branch volume of 0.6 was used for all species (e.g. Cannell, 1984). Using a logarithmic function a DBH-height relationship was determined separately for species represented by more than 20 individuals, while individuals of other species were pooled:

$$h = a + b\ln(d)$$

where h is the height and d is DBH.

4. Results

The felling treatments caused considerable damage to the remaining stands, and at the first evaluation in 1994 the annual basal area mortality rate was 24–41% for the heavy treatment, and 11–15% for the moderate treatment (Table 2, Fig. 1). In years succeeding the felling, the treated plots of the low restinga and tahuampa exhibited an annual mortality rate higher than the untreated plots (Fig. 1). The annual mortality rates of the untouched plots were relatively high in terms of stems and basal area (1.6–5.2% per year and 0.9–4.4% per year, respectively; Table 2, Fig. 1). Annual ingrowth rates also varied considerably with the highest rates in treated plots, in years following treatments (Table 2).

The average annual stem mortality rates were relatively constant across diameter classes for all three forest types. However, the large individuals in the high restinga had elevated annual mortality rates, and the medium sized trees in the tahuampa had lower than average annual mortality rates (Fig. 2).

Dead individuals during the period 1993–1997 tended to be clumped in the untreated plots (3, 6, and 9) of all three forest types (Fig. 3). The Morisita index of dispersion (I_δ) revealed a significant departure from random dispersion towards clumping for all plots and quadrat sizes ($I_\delta > 1$; $P < 0.001$; Fig. 3).

The annual basal area growth was 0.71–1.16 m^2 per year, with a tendency for the highest absolute and relative growth rates in the low restinga (Table 2, Fig. 4). No decrease in basal area growth was observed in the treated plots.

Table 2
Stocking, mortality, recruitment and growth of individuals ≥10 cm DBH in permanent sample plots located in high restinga (plots 1–3), low restinga (plots 4–6), and tahuampa (plots 7–9) flood plain forests at Braga–Supay and Lobillo[a]

Plot	Year	Period (years)	Individuals (stems)			Basal area (m^2)				DBH increment (mm per year)
			Absolute	Recruitment	Mortality	Absolute	Recruitment	Mortality	Growth of surviving trees[b]	
1	93		469			25.07				
		1.04		26 (6.5)	100 (23.0)		0.23 (1.4)	8.72 (41.1)	–	–
1	94		395			17.06				
		1.13		49 (10.7)	11 (2.5)		0.46 (2.4)	0.28 (1.5)	1.55 (4.3)	5.4 ± 0.7
1	95		433			18.23				
		1.92		88 (10.3)	28 (3.5)		1.00 (2.9)	0.60 (1.7)	1.86 (5.2)	6.2 ± 0.8
1	97		493			20.39				
2	93		447			25.03				
		1.04		33 (7.5)	39 (8.8)		0.30 (1.3)	3.62 (15.0)	–	–
2	94		441			22.30				
		1.17		49 (9.3)	14 (2.8)		0.45 (1.8)	0.75 (2.9)	1.69 (3.6)	5.3 ± 0.7
2	95		476			23.00				
		1.92		49 (5.5)	32 (3.6)		0.58 (1.4)	1.11 (2.6)	1.62 (3.7)	5.5 ± 0.7
2	97		493			23.95				
3	93		452			25.19				
		1.04		23 (4.9)	12 (2.6)		0.20 (0.8)	0.43 (1.7)	–	–
3	94		463			25.67				
		1.17		30 (5.5)	9 (1.7)		0.37 (1.3)	0.86 (2.9)	1.66 (3.0)	4.2 ± 0.5
3	95		484			26.08				
		1.92		29 (3.3)	46 (5.2)		0.25 (0.5)	2.12 (4.4)	1.86 (3.9)	4.5 ± 0.6
3	97		467			26.02				
4	93		526			19.88				
		1.13		36 (6.9)	79 (14.5)		0.30 (1.8)	4.73 (24.1)	–	–
4	94		483			16.27				
		1.04		63 (12.1)	15 (3.0)		0.60 (3.7)	0.80 (4.9)	1.99 (6.0)	5.9 ± 0.6
4	95		531			17.17				
		1.92		102 (10.0)	47 (4.8)		0.99 (3.2)	1.46 (4.6)	2.23 (6.9)	6.8 ± 0.7
4	97		586			18.75				
5	93		601			23.67				
		1.00		36 (6.3)	43 (7.4)		0.32 (1.5)	2.51 (11.2)	–	–
5	94		594			22.30				
		1.04		52 (8.3)	19 (3.1)		0.50 (2.2)	0.86 (3.8)	1.98 (4.6)	5.5 ± 0.5
5	95		627			23.01				
		1.96		71 (5.9)	51 (4.3)		0.66 (1.6)	2.24 (5.2)	2.28 (5.3)	6.0 ± 0.5
5	97		645			23.57				
6	93		569			24.32				
		0.83		19 (4.0)	14 (3.0)		0.16 (0.8)	0.75 (3.7)	–	–
6	94		573			24.28				
		1.08		24 (3.9)	10 (1.6)		0.24 (0.9)	0.24 (0.9)	1.66 (3.6)	4.3 ± 0.4
6	95		587			25.34				
		1.92		31 (2.8)	22 (2.0)		0.28 (0.6)	0.50 (1.0)	2.13 (4.3)	4.4 ± 0.5
6	97		594			27.20				

Table 2 (*Continued*)

Plot	Year	Period (years)	Individuals (stems)			Basal area (m^2)				DBH increment (mm per year)
			Absolute	Recruitment	Mortality	Absolute	Recruitment	Mortality	Growth of surviving trees[b]	
7	93		521			27.14				
		1.08		7 (1.4)	72 (13.7)		0.06 (0.3)	7.52 (29.9)	–	–
7	94		456			19.94				
		1.08		41 (8.7)	42 (8.9)		0.45 (2.2)	1.52 (7.3)	1.75 (4.3)	5.3 ± 0.4
7	95		456			20.31				
		1.92		58 (7.2)	65 (8.0)		0.53 (1.5)	2.09 (5.7)	1.83 (5.0)	6.6 ± 0.5
7	97		449			20.46				
8	93		507			28.84				
		1.08		9 (1.7)	36 (6.8)		0.07 (0.3)	3.56 (12.1)	–	–
8	94		479			25.83				
		1.08		33 (6.6)	32 (6.4)		0.28 (1.0)	1.11 (4.1)	1.68 (3.1)	4.4 ± 0.3
8	95		481			26.16				
		1.92		38 (4.3)	36 (4.1)		0.34 (0.7)	2.48 (5.2)	1.55 (3.3)	4.6 ± 0.4
8	97		483			25.51				
9	93		532			26.91				
		1.08		11 (1.9)	10 (1.8)		0.09 (0.3)	0.40 (1.4)	–	–
9	94		533			27.15				
		1.13		26 (4.4)	18 (3.1)		0.25 (0.9)	1.29 (4.3)	2.03 (3.5)	4.2 ± 0.4
9	95		541			27.55				
		1.92		27 (2.7)	27 (2.7)		0.24 (0.5)	1.21 (2.3)	1.70 (3.3)	4.0 ± 0.4
9	97		541			28.24				

[a] Plots 1, 4 and 7 were treated with a heavy felling, plots 2, 5 and 8 with a moderate felling, while plots 3, 6 and 9 were untreated. Numbers are mean annual rates of mortality, recruitment or growth. DBH increment shows mean and 95% confidence limits in parentheses.

[b] First figure for each plot refer to the period 1993–1995.

The average annual diameter increment varied from 4.0 to 6.8 mm per year calculated for single plots in the two measurement periods, with 95% confidence limits of 0.3–0.8 mm per year (Table 2). There was a pronounced tendency for an increased diameter growth with increasing felling intensities (Fig. 5). Furthermore, in most plots the diameter increment was highest in the period 1995–1997 (Fig. 5). The pronounced difference in diameter increments in plot 7 between the two measurement periods may partly be due to the

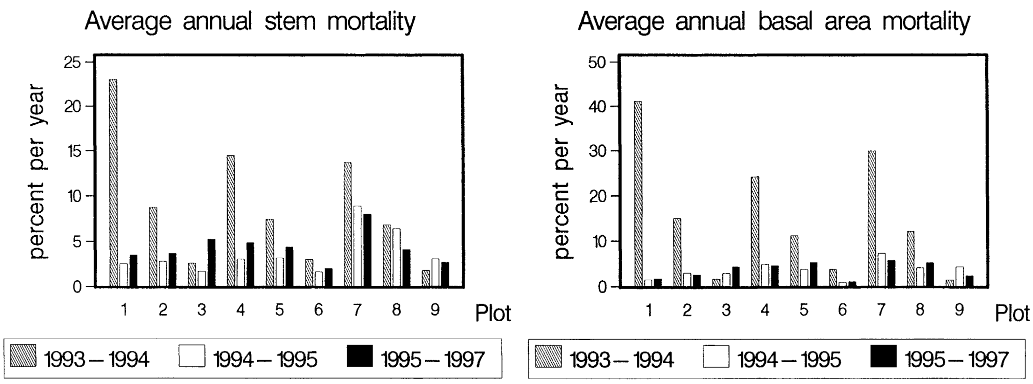

Fig. 1. Annual rates of stem and basal area mortality. Data from permanent sample plots located in high restinga (plots 1–3), low restinga (plots 4–6), and tahuampa (plots 7–9) flood plain forests at Braga–Supay and Lobillo, Peruvian Amazon. Plots 1, 4, and 7 were treated with a heavy felling, plots 2, 5, and 8 with a moderate felling, while plots 3, 6, and 9 are untreated.

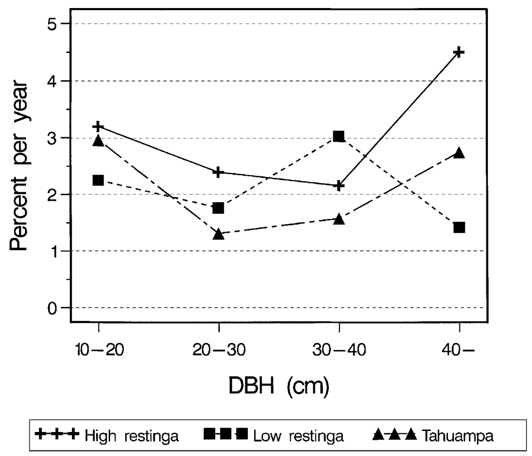

Fig. 2. Average annual stem mortality rates in diameter classes for untreated permanent sample plots located in flood plain forests at Braga–Supay and Lobillo, Peruvian Amazon.

later felling treatment in the tahuampa forest (August, 1994).

In the untreated plots (3, 6, and 9), the average annual stem and basal area mortality rates were highest for the high restinga (plot 3; Table 3). The low restinga and the tahuampa (plots 6 and 9) had almost equal average annual stem mortality rates, but the average annual basal area mortality rate in the low restinga was considerably lower than in the tahuampa (Table 3). Average annual recruitment rates for stems and basal area were highest in the high restinga (Table 3). Stand half-life and doubling time were lowest in the high restinga (22 and 16 years, respectively), and compared to other neotropical rain forests this forest ranged among the most dynamic (Table 3). In all three forest types the sums of the average annual basal area growth and recruitment rates exceeded the average annual mortality rates, indicating that all three forest types were in a growing phase, which was most conspicuous in the low restinga forest type (Table 3).

Commercially valuable timber species had a density of 44–89 trees per hectare (9–17% of the total stem number). These individuals accounted for a considerable basal area of 2.6–10.0 m^2/ha (10–40% of the total basal area) and a volume of 59–286 m^3/ha (Table 4). The increment in basal area and volume of surviving individuals was 0.1–0.3 m^2/ha per year and 2–9 m^3/ha per year, corresponding to growth rates of 2.4–5.3% per year (Table 4). The basal area growth rates of timber species were lower than for all species together, despite higher mean annual diameter increments of the timber trees (compare Table 2 and Table 4).

5. Discussion

5.1. Mortality and recruitment

The average annual mortality rates in the untreated plots at Braga–Supay and Lobillo (stem mortality 2.20–3.16% per year; basal area mortality 1.89–3.00% per year) were relatively high compared to mortality rates in neotropical lowland rain forests (Table 3; Condit et al., 1995), and other tropical lowland rain forests (Swaine et al., 1987a; Swaine et al., 1987b; Phillips and Gentry, 1994; Phillips et al., 1994). Lower mortality rates were not observed in the treated plots where basal areas were lower (Table 2, Fig. 1), although this could have been expected due to a lower competition in these plots. Evidently, the felling has contributed to an elevated mortality rate lasting several years after the treatments. The average annual recruitment rates of the untreated plots were also high (stem recruitment 2.99–4.57% per year; basal area recruitment 0.58–0.81% per year; Table 3). Consequently, the stand half-lives and doubling times for the untreated plots were low, indicating that all three forest types were dynamic. Actually, they were all among the most dynamic of neotropical lowland rain forests from which data were available (Table 3).

Phillips et al. (1994) found that the average of mortality and recruitment rates ("dynamism") explained more of the species richness of the 25 humid tropical forests they studied, than did primary environmental factors related to soils and climate. Gentry (1988, 1992) identified the latter as best predictors of species richness in a study not including factors related to forest dynamics processes. However, the relatively low species richness of the Braga–Supay and Lobillo flood plain forests (90–125 species per 500 stems; Nebel et al., 2001a) combined with the high mortality and recruitment rates did not correspond with the correlation between these two factors observed by Phillips et al. (1994). One explanation could be that the forests at Braga–Supay and Lobillo were still in a strong succession development, whereas the data set of Phillips et al. (1994) excluded sites where the mortality and growth were temporarily elevated. Meanwhile, the forest structure and the presence of

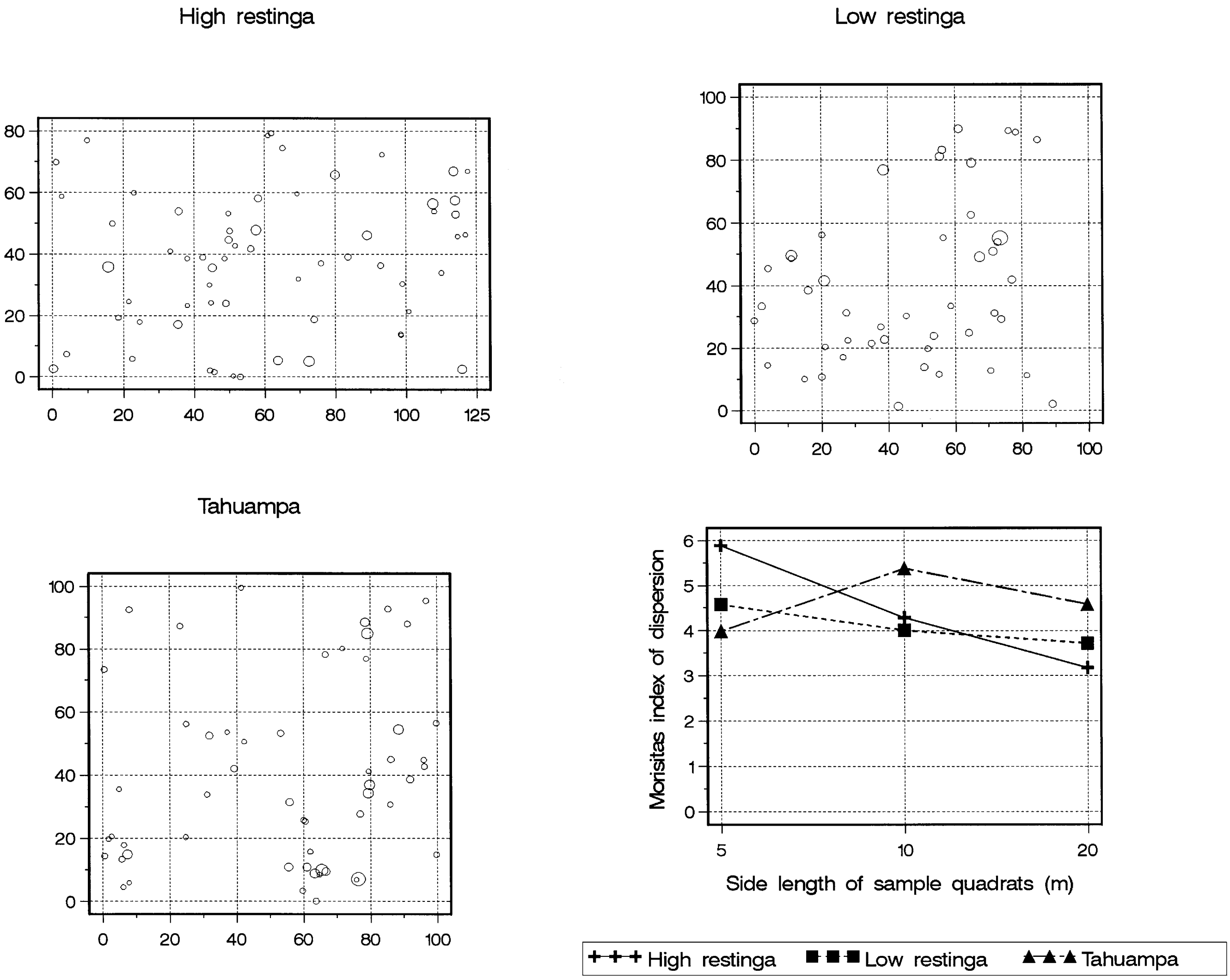

Fig. 3. Dispersion of dead individuals in untreated permanent sample plots over the period 1993–1997 in three flood plain forests at Braga–Supay and Lobillo, Peruvian Amazon. Side lengths of scatter plots in metre, and size of circles according to diameter of dead individuals. Corresponding values for the Morisita index of dispersion (I_δ).

large trees and species characteristic of later succession stages in the Braga–Supay and Lobillo forests (Nebel et al., 2001a) indicated that these forests were all well-developed. Flooded forests normally contain fewer species than their non-inundated counterparts (Gentry, 1982, 1986; Campbell et al., 1986; Balslev et al., 1987; Junk, 1989; Dumont et al., 1990; Freitas, 1996a, 1996b; Worbes, 1997; Nebel et al., 2001a). This could be a likely explanation why the Braga–Supay and Lobillo forests diverged from the correlation between forest dynamics and species richness observed by Phillips et al. (1994). Consequently, our results were not at odds with the hypothesis of Phillips et al. (1994) proposing that high productivity helps maintain species richness through promoting frequent, spatially unpredictable small-scale disturbances. Flood plain forests may maintain lower species richness, as many species do not establish and survive at flooded sites. This is also indicated by the relatively low species richness at high mortality and recruitment rates for the flood plain forest sites at Manú and Tambopata in Peru mentioned in the data set of Phillips et al. (1994).

Analyses of mortality and recruitment rates based on stem density and basal area provide limited information, as the numerically similar figures may be obtained from different situations (Lieberman et al.,

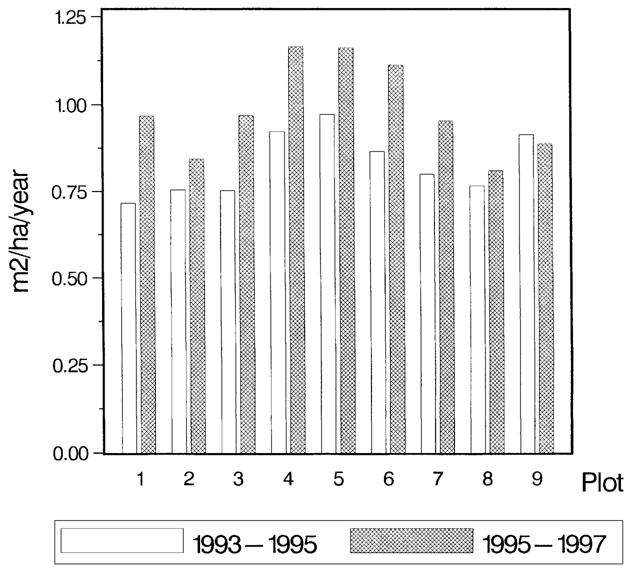

Fig. 4. Average annual basal area growth (m^2/ha per year) in permanent sample plots located in high restinga (plots 1–3), low restinga (plots 4–6), and tahuampa (plots 7–9) flood plain forests at Braga–Supay and Lobillo, Peruvian Amazon. Plots 1, 4, and 7 were treated with a heavy felling, plots 2, 5, and 8 with a moderate felling, while plots 3, 6, and 9 are untreated.

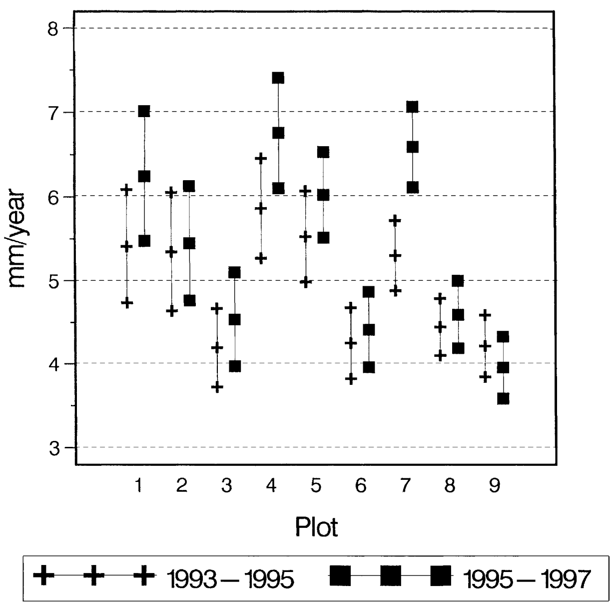

Fig. 5. Mean and 95% confidence limits for the average annual diameter increment (mm per year) of individuals ≥10 cm DBH in permanent sample plots located in high restinga (plots 1–3), low restinga (plots 4–6), and tahuampa (plots 7–9) flood plain forests at Braga–Supay and Lobillo, Peruvian Amazon. Plots 1, 4, and 7 were treated with a heavy felling, plots 2, 5, and 8 with a moderate felling, while plots 3, 6 and 9 are untreated.

1985a, 1990). At one extreme early succession forest stages may be dominated by randomly spaced and density-dependent mortality of standing small or medium sized individuals, which does not cause many other trees to fall in a gap forming process. On the other hand, later succession stages may be dominated by the gap dynamics where gap formation dominates and mortality and recruitment patterns tend to be clumped (e.g. Brokaw, 1982; Lieberman et al., 1985a; Korning and Balslev, 1994a; Van der Meer and Bongers, 1995a).

Therefore, an alternative or complement to studying the mortality and recruitment rates of stems or basal area is to investigate gap formation and regeneration, e.g. their rates, patterns and processes (e.g. Brokaw, 1982; Lieberman et al., 1985a; Korning and Balslev, 1994a; Van der Meer and Bongers, 1995a). Gap formation studies are impaired by time consuming registrations, and estimates vary much with gap definitions. For example Van der Meer and Bongers (1995b) found annual gap formation rates in the range of 0.22–2.87% per year when applying three different gap definitions on the same area in a lowland tropical rain forest in French Guiana. Modes of tree death may provide useful ecological information about the ecosystems under study, e.g. falling trees dominate in gap dynamics succession stages and snapped trees in forests exposed to wind damage. Deviations from constant mortality rates over diameters may indicate gap formation if elevated mortality occur among large individuals. Similarly, clumping of dead individuals indicates gap formation, and aggregated occurrence of regeneration suggests that rejuvenation takes place in gaps. In both cases, the horizontal distribution of individuals must be known, and analyses of the regeneration also demand that small sized individuals are inventoried.

At Braga–Supay and Lobillo the higher than average mortality rate of large sized individuals in the untreated high restinga forest (plot 3; Fig. 2) indicated that this forest is in a late succession phase, as large sized trees had elevated probabilities of dying. Conversely, the lower than average mortality rate among large individuals in the untreated low restinga forest plot (Fig. 2) suggests an earlier succession stage. The dispersion towards clumping of dead trees in all three forest types (Fig. 3) indicated that gap dynamics phases were reached, and there was no evidence in these data that the low restinga was a younger forest type.

Table 3
Mortality, recruitment and growth in neotropical lowland rain forests[a]

	Ref. no.	Area (ha)	Min. DBH (cm)	Time period (years)	No. of enumerations	Mortality rate (% per year)	Stand half-life (year)	Recruitment rate (% per year)	Doubling time (year)	Basal area mortality		Basal area recruitment		Basal area growth of surviving trees	
										(m^2/ha per year)	(% per year)	(m^2/ha per year)	(% per year)	(m^2/ha per year)	(% per year)
Amazon															
Brazil, Manaus, Tierra firme	1	5.0	10	1981–1986 (5)	1	1.16	60	0.91	76	–	–	–	–	–	–
Brazil, Belem, clay	2	2.0	10	1956–1971 (15)	1	1.84	38	0.81	86	–	–	–	–	–	–
Ecuador, Cuyabeno, Tierra firme, Plot 1	3	1.0	10	1988–1990 (2.5)	1	1.05	66	3.12	22	0.44	1.65	0.20	0.76	0.92	3.38
Ecuador, Añangu, Tierra firme, Plot 2	3	1.0	10	1986–1990 (4.9)	1	1.89	37	1.81	38	0.37	1.73	0.10	0.49	0.63	2.89
Ecuador, Añangu, Tierra firme, Transect 1	3	1.1	10	1982–1990 (8.5)	1	1.88	37	–	–	0.74	2.41	–	–	0.63	2.09
Ecuador, Añangu, Flood plain, Transect 2	3	1.0	10	1982–1990 (8.5)	1	3.08	23	–	–	1.28	4.13	–	–	0.75	2.60
Ecuador, Jatun Sacha, Upland	2	1.0	10	1987–1992 (5.0)	1	1.46	48	1.63	43	–	–	–	–	–	–
Peru, Cocha Cashu, Flood plain	4	0.9	10	1974–1985 (10)	1	1.79	39	0.96	73	–	–	–	–	–	–
Peru, Braga–Supay, Flood plain, High restinga, Plot 3[b]	5	1.0	10	1993–1997 (4.1)	2	3.16	22	4.57	16	0.83	3.00	0.20	0.81	0.85	3.51
Peru, Braga–Supay, Flood plain, Low restinga, Plot 6[b]	5	1.0	10	1993–1997 (3.8)	2	2.20	32	3.56	20	0.39	1.89	0.18	0.68	0.99	3.79
Peru, Lobillo, Flood plain, Tahuampa, Plot 9[b]	5	1.0	10	1993–1997 (4.1)	2	2.49	28	2.99	24	0.70	2.69	0.14	0.58	0.91	3.73
Peru, Mishana, Sandy	2	0.95	10	1983–1990 (7.58)	1	1.62	43	1.23	56		–	–	–	–	–
Peru, Tambopata, Waterlogged swamp	2	0.6	10	1983–1990 (7)	1	0.70	99	0.94	74	–	–	–	–	–	–
Peru, Tambopata, Upper floodplain	2	0.95	10	1983–1991 (7.75)	1	1.84	38	2.83	25	–	–	–	–	–	–
Peru, Tambopata, Old floodplain	2	1.0	10	1983–1991 (7.75)	1	2.85	24	2.37	29	–	–	–	–	–	–
Peru, Tambopata, Upland	2	1.0	10	1979–1991 (11.67)	5	1.97	35	1.96	35	–	–	–	–	–	–
Peru, Tambopata, Upland	2	2.0	10	1983–1991 (7.75)	1	2.69	26	2.25	31	–	–	–	–	–	–
Peru, Yanamono, Old floodplain	2	1.0	10	1983–1993 (9.75)	4	2.81	25	2.32	30	–	–	–	–	–	–
Venezuela, San Carlos, Tierra firme[b]	6	1.0	10	1975–1985 (10)	2	1.18	59	1.74	40	–	–	–	–	–	–
Central America and the Caribbean															
Costa Rica, La Selva, Plot 1	7	4.4	10	1969–1982 (13)	1	2.34	30	2.12	33	0.53	2.07	0.11	0.46	0.36	1.43
Costa Rica, La Selva, Plot 2	7	4.0	10	1969–1982 (13)	1	2.62	26	2.71	26	0.64	2.15	0.14	0.53	0.23	0.83
Costa Rica, La Selva, Plot 3	7	4.0	10	1969–1982 (13)	1	2.91	24	2.99	23	0.76	3.05	0.20	0.88	0.25	1.12
Panama, Barro Colorado Island	8	1.5	2.5	1968–1978 (10)	1	2.21	32	0.90	77	–	–	–	–	–	–
Panama, Barro Colorado Island, Young forest	9	5.0	19	1975–1980 (5)	1	1.83	38	–	–	–	–	–	–	–	–
Panama, Barro Colorado Island, Old forest	9	2.0	19	1975–1980 (5)	1	1.09	64	–	–	–	–	–	–	–	–
Panama, Barro Colorado Island, Old-growth	10	50.0	1	1982–1985 (3)	1	3.02	23	4.48	16	–	–	–	–	–	–

[a] References: (1) Rankin-de-Mérona et al. (1990); (2) Phillips et al. (1994) and Phillips and Gentry (1994); (3) Korning and Balslev (1994a); (4) Gentry and Terborgh (1990); (5) this study; (6) Uhl et al. (1988); (7) Lieberman et al. (1985a, 1990); (8) Lang and Knight (1983); (9) Putz and Milton (1982); (10) Hubbell and Foster (1990).

[b] Rates of mortality, recruitment, and growth are averages for more than one period.

Table 4
Stocking and growth of individuals ≥10 cm DBH of commercial timber species in permanent sample plots located in high restinga (plots 1–3), low restinga (plots 4–6), and tahuampa (plots 7–9) flood plain forests at Braga–Supay and Lobillo, Peruvian Amazon[a]

Plot	Number of individuals	Basal area (m^2/ha)	Volume (m^3/ha)	Basal area growth (m^2/ha per year)	Basal area growth rate (% per year)	Volume growth (m^3/ha per year)	Volume growth rate (% per year)	DBH increment (mm per year)
1	52	6.0	146	0.3	4.3	6	4.3	9.0 ± 3.0
2	64	6.2	136	0.2	2.7	4	2.7	6.2 ± 1.6
3	74	10.0	240	0.3	3.3	8	3.4	6.8 ± 1.9
4	47	4.4	116	0.2	4.9	6	5.3	7.3 ± 2.3
5	73	7.0	181	0.2	2.7	5	2.5	6.9 ± 1.9
6	75	9.1	286	0.3	3.3	9	3.0	6.2 ± 1.8
7	44	2.6	59	0.1	3.2	2	3.3	5.5 ± 1.3
8	66	4.7	105	0.1	2.4	3	2.5	4.1 ± 0.9
9	89	6.1	145	0.2	3.0	4	3.1	3.9 ± 1.0

[a] Plots 1, 4, and 7 were treated with a heavy felling, plots 2, 5, and 8 with a moderate felling, while plots 3, 6, and 9 were untreated. Figures are mean values, and diameter increment shows mean and 95% confidence limits.

5.2. Growth

The basal area growth of the Braga–Supay and Lobillo forests was considerable, and in the plots where felling treatments were carried out, there was no tendency for a lower average annual basal area growth than in the untreated plots (Tables 2 and 3, Fig. 3). This showed that the forests supported the applied felling treatments resulting in basal area mortality rates up to 41% during the first year without significant temporary growth losses. There was a tendency for higher basal area growth in the last measurement period (1995–1997; Fig. 3), which indicated more favourable growth conditions, perhaps caused by briefer inundations. The absolute and relative growth compared well with registrations from other neotropical lowland rain forests (Table 3), and tended to be at the high end. However, it must be noticed that some of the studies used long measurement periods and only one enumeration, implying that growth of trees dying in the period was omitted.

The increasing average diameter growth with increasing felling intensity (Table 2, Fig. 3) reflected that the close to constant basal area growth was dispersed to smaller basal areas of the remaining stands. Likewise, for most plots the second measurement period (1995–1997; Fig. 3) had the highest mean diameter increment. The diameter increments of 4.0–6.8 mm per year on the average in treated and untreated plots matched results from other neotropical lowland rain forests. For instance, Worbes et al. (1992) analysed annual growth ring formations in flood plain forest trees from the central Amazon. They determined average diameter growth and wood density for dominant trees in four forest succession stages: pioneer (9.4 mm per year, 0.44 g/cm^3), early secondary (4.3 mm per year, 0.46 g/cm^3), late secondary (3.0 mm per year, 0.56 g/cm^3) and climax (2.0 mm per year, 0.86 g/cm^3). Korning and Balslev (1994b) measured mean diameter growth for 15 midcanopy and canopy species in flood plain and terra firme forests in Ecuador: 0.7–11.1 mm per year, mean 3.0 mm per year. Lieberman et al. (1985b) projected growth of 32 subcanopy and canopy species in a Central American lowland rain forest and determined median growth rates: 0.6–13.4 mm per year, mean 3.3 mm per year. Clark and Clark (1992) studied diameter development of the populations of six tree species in a Central American forest, and determined median diameter increments for individuals ≥10 cm DBH in the range 0.8–12.3 mm per year across diameter classes. They found significant year-to-year variation in the diameter growth of the species they studied, and low and high auto-correlation in diameter growth for small (up to 10 cm DBH) and large (≥10 cm DBH) individuals, respectively.

The stocking and growth of commercial timber species of the present study varied much between the 1 ha plots and forest types (Table 4), but the levels were generally high compared with the results from other natural tropical rain forests (e.g. Lamprecht, 1989, 1993; Silva, 1989). The high stocking of commercial species suggested that a considerable flexibility can be attained in the logging operations, implying that over-exploitation of populations of single species can be prevented. It seems reasonable that growth of more than 5 m^3/ha per year can be attained in the restinga forests, indicating that sustained yield in polycyclic silvicultural systems can be maintained with relatively short cutting cycles. Even in the heavy treatment there was no indication of loses of growth potential, and the residual stand of commercial species responded with elevated DBH increment and growth rates. Manipulation of the floristic composition towards an increased representation of commercial species and introduction of additional species to the market may further increase the timber yields of the flood plain forests.

5.3. Forest succession

Amazonian flood plain forests are influenced by dynamic fluvial processes causing large perturbations of the environment, and by complex environmental conditions linked to the flooding. This creates a patchy landscape with inter-mixed and often relatively small habitats characterised by different environmental conditions and succession stages (e.g. Foster et al., 1986; Salo et al., 1986; Worbes et al., 1992; Worbes, 1997; Kvist and Nebel, 2001). Analyses of the growth conditions, the floristic composition, and the structure of the Braga–Supay and Lobillo forests indicated that they represented different types, probably due to differing average annual flooding periods and establishment histories. They all contained large and old trees, but the species composition of the low restinga suggested that this might be a younger succession stage (Nebel et al., 2001a). The forest dynamics data from the untreated plots partly supported this impression. All three forest types were in a growing phase, where basal area ingrowth and growth exceed the basal area mortality. This tendency was most pronounced for the low restinga, while the high restinga and tahuampa were closer to a homeostatic stage

Table 5
Some special features of Peruvian flood plain forests and their implications for management

Feature	Characteristics in the flood plain environment	Implications for forest management and conservation
Community structure	Interactions between populations from terrestrial and aquatic environments	Possible impacts from forest interventions on the aquatic environment should be considered, e.g. feeding and breeding of fish populations
Soil chemical and physical conditions	Generally fertile alluvial soils. Patchy distribution of soil properties due to vertical and horizontal variation according to the sedimentation history. For example causing a variable fertility and drainage pattern	Little risk of soil nutrient depletion in connection to biomass removal. The soil related production potential and the vegetation composition and structure change much even within small distances
Flooding	Changes in flooding exposure according to the terrain level, implying that flooding tolerance of plants determine their growth success, especially at juvenile stages. Generally a decreased plant production potential at long inundations. Presence of vegetation types specialised to different degrees of flooding	Management must consider that some species are specialised to certain inundation patterns. Large individuals are generally more resistant to flooding than small, and a successful recruitment may be promoted through advancing growth in juvenile stages by liberation thinning or through planting of large sized individuals
Vegetation disturbance regime	Large perturbations on a limited proportion of each habitat caused by fluvial processes create flood plain forests which apparently have a high resilience. Many flood plain forests are in relatively early succession stages	Relatively rough forest interventions can take place within the range of naturally occurring perturbations, but only on a limited proportion of each habitat. A desirable forest succession stage may be kept through continuous interventions
Vegetation dynamics	Rates of growth, mortality and recruitment are generally high compared to other tropical rain forest sites. Growth responses without loss of growth potential to relatively heavy interventions	A high production potential and a good response to interventions
Location	Proximity to the natural river infrastructure system	An easy access and low timber extraction costs by floating or barges/ships
Habitat size	Often small dispersed patches of uniform environments and succession stages	Management systems must be able to handle and address small and dispersed production units

(Table 3). Furthermore, a lower than average mortality rate in the largest diameter class in the low restinga indicated a young succession stage (Fig. 2), although the dispersion of dead individuals showed a clumped pattern (Fig. 3). There was therefore evidence that the high restinga and the tahuampa forests were in a growing phase and characterized by gap dynamics, while the low restinga was probably younger.

5.4. Implications for forest management and conservation

Several special features related to the biology and geography of the flood plain forests have implications for forest management (Table 5).

The productivity can be high and rough forest interventions can be carried out within the range of naturally occurring perturbations, although only on a limited proportion of each habitat at a time. Factors as flooding stress, possible impacts on other parts of the community (e.g. fish populations) and planning and logistic obstacles related to the patchy habitat occurrence impede management. The extent to which these features and their implications for management can be extrapolated to other Amazonian flood plain forests is not known. The diverse and complex environmental conditions of the Amazonian flood plains suggest that care should be taken in basing land-use planning on generalised results. From an ecological point of view a large scale classification of the flood plains according to important environmental and vegetative factors as flooding period, origin of landscape, age since establishment and vegetation composition and structure is a prerequisite for a land-use planning to take place. Remote sensing techniques may be helpful in this respect. In addition, more specific knowledge on the ecology of some of the most used and extracted species for timber and non-timber forest products is needed.

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