

VEGETATION SUCCESSION OF LOGGED FOREST IN THE WESTERN ALLUVIAL PLAINS OF VENEZUELA

JR Lozada^{1,*}, E Arends¹, D Sánchez¹, A Villarreal¹, P Soriano² & M Costa²

¹Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes, Vía Chorros de Milla, Mérida 5101, Venezuela

²Jardín Botánico de la Universidad de Valencia, Calle Quart, 80, Valencia 46008, Spain

Received February 2011

LOZADA JR, ARENDS E, SÁNCHEZ D, VILLARREAL A, SORIANO P & COSTA M.

2012. Vegetation succession of logged forest in the western alluvial plains of Venezuela. Nearly all forests in the Venezuelan alluvial plains are converted to agricultural lands. However, in forest reserves, logging is a selective extraction activity that disturbs part of the ecosystem. This work was aimed at studying floristic composition changes over longer periods of time in a forest with different logging intensities. We measured 11 plots distributed in random block design of 1 ha each. The importance value index (IVI) was calculated for all species and was used in a canonical correspondence analysis to evaluate species behaviour. *Cecropia peltata* and *Inga* sp. dominated the first successional stage attaining a maximum IVI close to 12 years but showed clear decline thereafter. The next successional phase was dominated by late secondary species such as *Triplaris americana* and *Guazuma ulmifolia*. Climax species such as *Pouteria reticulata* and *Pachira quinata* showed drastic reduction in importance and very slow recovery. This study was based on 16-year-observation period, a rare work which could make use of such long period of direct observation. Our results could be used to guide ecological restoration in deforested areas. Forest management strategies should be redrawn to make it a sustainable option.

Keywords: Caparo Experimental Station, forest management, ecological behaviour, logging impact, ecological restoration

LOZADA JR, ARENDS E, SÁNCHEZ D, VILLARREAL A, SORIANO P & COSTA M.

2012. Sesaran vegetasi bagi hutan sudah dibalak di dataran alluvium di barat Venezuela. Hampir kesemua hutan di dataran alluvium Venezuela ditukar kepada tanah pertanian. Namun di hutan simpan, pembalakan merupakan aktiviti pengeluaran memilih yang mengganggu sebahagian sahaja ekosistemnya. Kajian ini bertujuan untuk meneliti perubahan komposisi flora di dalam hutan yang mengalami kadar pembalakan yang berlainan untuk jangka masa yang lebih panjang. Kami mengkaji 11 plot masing-masing bersaiz 1 ha dalam taburan reka bentuk blok rawak. Indeks nilai kepentingan (IVI) dikira untuk semua spesies dan digunakan dalam analisis hubung kait canon bagi menilai kelakuan spesies. *Cecropia peltata* dan *Inga* sp. menguasai tahap sesaran pertama dan mencapai IVI maksimum selepas hampir 12 tahun tetapi berkurangan selepas itu. Fasa sesaran seterusnya dikuasai oleh spesies sekunder lewat seperti *Triplaris americana* dan *Guazuma ulmifolia*. Spesies klimaks seperti *Pouteria reticulata* dan *Pachira quinata* menunjukkan penurunan kepentingan yang mendadak dan pemulihan yang sangat lambat. Kajian ini berdasarkan tempoh pemerhatian selama 16 tahun, satu kerja yang jarang dapat menggunakan tempoh pemerhatian terus yang begitu lama. Keputusan boleh dijadikan panduan pemuliharaan ekologi di kawasan pembasmian hutan. Strategi pengurusan hutan patut dikaji semula untuk menjadikannya pilihan yang mampan.

INTRODUCTION

Venezuela has the 10th highest deforestation rate in the world (FAO 2011). Almost all lowland forest north of the Orinoco River has disappeared (Bontemps et al. 2010). Deforestation occurs mainly due to agricultural activities (Lozada 2007). However, timber harvest in forest reserves is selective and logged forests still have a high level of tree cover.

Logging is done selectively because neotropical forests are very heterogeneous and only a

few species have commercial value. However, important impacts take place on the structure of the logged-over forest communities. In West Malaysia, felling of 3.3% of the trees destroyed an additional 47.6% of trees (Johns 1988). In Brazil, it has been found that for every logged tree, between 26 and 51 others are damaged (Verissimo et al. 1992, Johns et al. 1996).

In the Caparo Experimental Station, located in the western Venezuelan plains, Lozada and

*E-mail: jolozada@ula.ve

Arends (2000) established a permanent plot system to evaluate the impact of different logging intensities on individuals ≥ 10 cm dbh (diameter at breast height, 1.3 m height). When cutting 91 trees larger than 20 cm dbh, 79 additional trees died. In a treatment similar to conventional logging, seven trees larger than 60 cm dbh were felled but 51 additional trees disappeared (larger than 10 cm dbh).

Long-term studies on the impact of logging on floristic composition and structure (abundance and basal area) of the remaining stand are scarce (Verburg & Van Eijk-Bos 2003); some reports are controversial. For example, Uganda's forest did not recover its original structure 50 years after logging (Plumptre 1996). However, there are reports of successful recoveries of managed forests in Brazil (Magnusson et al. 1999) and Suriname (De Graaf 2000).

Other works have shown that due to successional dynamics, logged forests recover mainly with light-demanding secondary species. Logged forests up to 19 years old are reported to be partly dominated by the pioneer *Cecropia peltata*, while *Pachira quinata* (the main dominant species in the old-growth forest) is practically absent from residual stands (Plonczak 1993, Kammesheidt 1994, 1998). Insufficient seed trees is critical in the regeneration process. Similar results were found by Ruschel (2008) in Tapajós, Brazil and Moret et al. (2008) in Caimital, Venezuela.

Animals are also important in tropical forest dynamics. They are responsible for pollination, dispersion, herbivory and seed predation. Logging reduces key resources (food, refuges and movement strata), produce ecophysiological barriers and diminish mammal populations (Ochoa 1997). However, some taxa are favoured because they are well adapted to disturbed forests. Decline in abundance of big predatory mammals is correlated with the increase of medium herbivory mammals, e.g. *Agouti* sp. (Redford 1992). Spiny rat (*Proechimys semispinosus*) is a great consumer of fruits and seeds; this rodent is favoured in disturbed ecosystems (Adler 2002). Forest disturbance affects pollinator bats of *P. quinata* (Stoner et al. 2007). In summary, logging modifies populations of birds, bats and rodents which have a fundamental role in successional process.

Now, there are doubts regarding the sustainability of 30-year cutting cycles. It is

believed that pioneer species still dominate during this period while the characteristic species of the old-growth forest are rare (De Oliveira 2005). Therefore, with further logging, pioneers are dominant and the proportion of old-growth species in the tree composition declines. One reason could be that gaps in logged forests are generally large, providing advantages for pioneer species regeneration (Quesada et al. 2009).

To enhance our knowledge on recovery processes in logged-over forests, we address in this paper the following questions: (1) what is the effect of different logging intensities on species composition?, (2) how is the change of key species with forest succession? and (3) what is the recovery of the logged forest in terms of basal area of different ecological groups?

MATERIALS AND METHODS

Study site

The Caparo Forest Reserve is located in the south-western region of the Barinas State in the western plains of Venezuela, comprising 174,000 ha (Figure 1). The experimental station is located in the north-western part of the reserve (70°45' W, 7° 30' N), covering approximately 7000 ha (Jurgenson 1994).

The average altitude is 140 m, with an unevenness of 2 m in 10 km (Vincent 1970, Jurgenson 1994). The annual average temperature is 24.8 °C and the annual total rainfall is 1753 mm. The precipitation is markedly seasonal. The dry season is between December and February (Lozada et al. 2006).

The study site is exposed to floods, with clay texture, slow drainage and strong mottles for iron oxides and magnesium due to the fluctuations of the phreatic level (Schargel 2005). The forests possess three to four strata, canopy of 25 m height and 70% cover. The most important species in the old-growth community are *Attalea butyracea*, *Pouteria reticulata*, *Trichanthera gigantea*, *Trichilia maynasia*, *Spondias mombim*, *Terminalia oblonga*, *Cordia thaisiana*, *Licania apetala* and *Clarisia biflora* (Guevara 2001).

Research design

A statistical design of random complete blocks was established with four treatments. Plot size was 100 m \times 100 m and total sampling area was

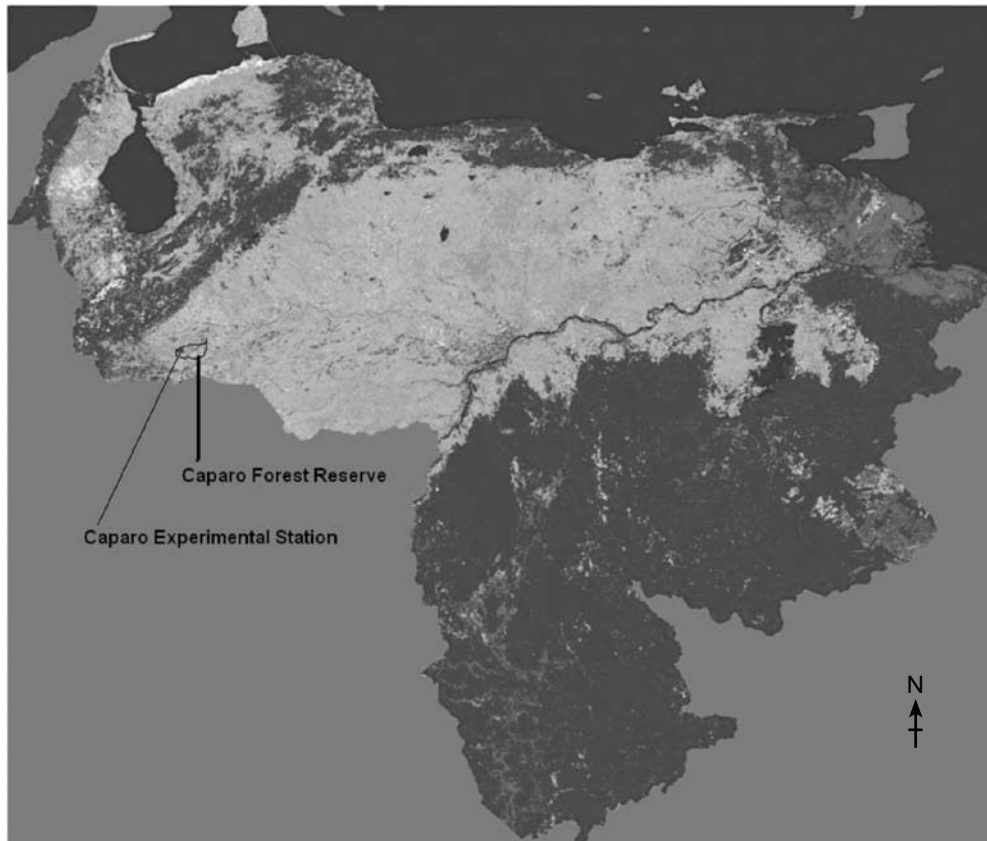


Figure 1 Map of the Caparo Experimental Station (Bontemps et al. 2010)

11 ha. Treatments were randomly located and applied according to the following prescriptions. Trees were cut above a certain minimum cutting diameter (mcd).

- T 9: mcd 20 cm (three plots)
- T 10: mcd 40 cm (three plots)
- T 11: mcd 60 cm (three plots)
- Control plots (two plots)

The treatments represented the intervention intensity. In other words, when lowering the mcd, a higher level of extracted biomass was expected and, therefore, a bigger impact.

First measurements were made in 1987 and treatments were applied immediately. Re-measurements were made at two- to three-year intervals, regardless of the dry or rainy season.

Sampling and data analysis

In each plot, all trees, climbers and palms with dbh ≥ 10 cm were measured. The importance value index (IVI) of each species was calculated (Curtis & McIntosh 1951) according to the following equation:

$$IVI = Ab\% + Fr\% + Dm\%$$

where Ab% is relative abundance, Fr% is relative frequency and Dm% is relative dominance.

The data were used to develop a canonical correspondence analysis (CCA). This multivariate analysis reveals variation patterns in the floristic composition of the communities that are explained by environmental variables. The classification axes are simultaneously axes of floristic and environmental variation; they can illustrate environmental gradients from ecological data sets (ter Braak 1987, ter Braak & Verdonschot 1995). To make the ordination, we took the floristic composition (with regard to species basal area), the age after logging and the disturbance level (percentage of basal area removed).

RESULTS

Logging effect

The plots 10r1, 10r3, 9r1 and 9r2 suffered high impact with 60 to 80% of the basal area removed (Table 1). The plots 10r2 and 11r2

Table 1 Disturbance level as loss of trees and basal area

Disturbance class	Plot	Original value		Loss after logging			
		Trees ha ⁻¹	Basal area (m ² ha ⁻¹)	Trees ha ⁻¹	%	Basal area (m ² ha ⁻¹)	%
Low	9r3	214	16.45	-24	11	-0.4	3
	11r1	251	16.20	-38	15	-1.9	12
	11r3	248	16.57	-9	4	-2.2	13
Medium	10r2	334	22.59	-77	23	-7.6	34
	11r2	323	23.62	-82	25	-9.2	39
High	10r1	309	21.81	-142	46	-13.8	63
	10r3	192	17.32	-68	35	-11.2	65
	9r1	273	21.89	-175	64	-16.6	76
	9r2	256	17.93	-171	67	-14.2	79

had intermediate impact, showing 34 to 40% reduction in basal area. The plots 9r3, 11r1 and 11r3 lost only 3 to 13% of their original basal area. These data reflected impact variability, from low to high levels. The greatest effect showed loss of 11–17 m² ha⁻¹.

In total, 98 species were recorded (Appendix). In the CCA, we selected the 21 most important species according to the IVI (Figure 2). For the observation period (16 years), the following trends could be seen.

- (1) *Ochroma pyramidale* and *Inga* sp. 1 were linked to medium to high perturbation rates and early successional stages (left and down of the graph).
- (2) *Cecropia peltata*, *Guazuma ulmifolia* and *Triplaris americana* preferred low to medium disturbance levels and intermediate to late stages (left and up of the graph).
- (3) To the right and down of the graph, the species seemed to be linked to non-perturbation conditions (*P. quinata*, *Pouteria reticulata*, *Swartzia leptopetala*, *C. thaisiana* and *Syagrus sancona*).
- (4) Some species seemed to be related to no perturbation conditions but advanced successional stages (right and up of the graph): *Sloanea terniflora*, *Ficus insipida*, *Inga marginata* and *Luehea seemannii*.
- (5) Some species were not evidently linked to disturbance level or age after logging (next to the centre of the graph): *T. gigantea*, *A. butyracea*, *Trichilia trifolia*, *Brosimum alicastrum*, *S. mombim*, *S. aubletianum* and *T. oblonga*.

Successional dynamics

Figures 3 to 5 illustrate the behaviour of six key species which show the development of logged forests. Disturbance level had effect on forest succession because pioneer species showed higher IVI values in high impact plots. *Cecropia peltata* and *Inga* sp. 1, in general, were absent from the old-growth forest. They reached maximum IVI at about 12 years after disturbance and declined thereafter.

Triplaris americana and *G. ulmifolia* also increased their importance after logging. However, they were also present in old-growth forest, though in smaller numbers.

In contrast, *P. reticulata* and *P. quinata* were rare after logging and their overall recovery process seemed slow.

Forest growth

Figure 6 shows the contribution of each group of species in stand recovery, expressed as share in basal area. In control plots, the growth of basal area was very slow.

In general, palms represented almost a third of the basal area and were not influenced by the different disturbance levels. The tolerant species represented a low portion in the overall basal area. This group was clearly affected by the high disturbance level and growth was very slow. The nomadic species had the largest share in basal area. In general, they showed acceptable recovery with any level of disturbance. The pioneer species

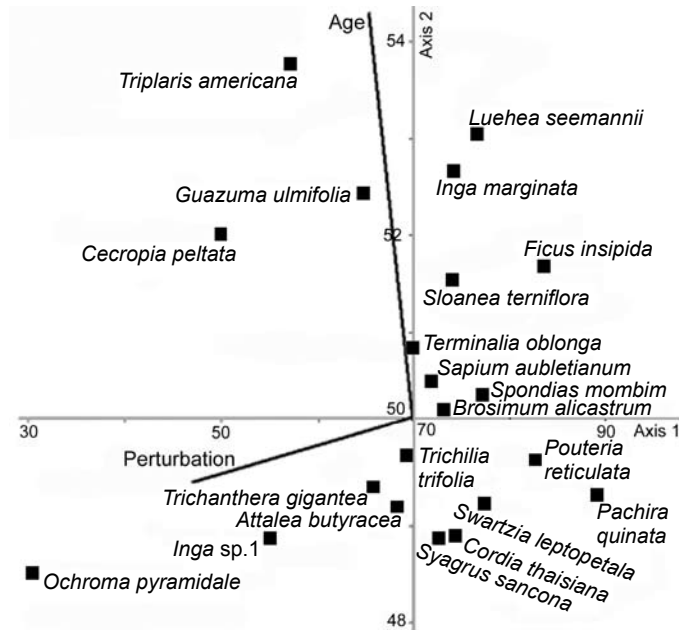


Figure 2 Results of the canonical correspondence analysis; black boxes indicate species position; bold lines designate environmental variables (perturbation level and age after logging); axes represent straight lines which absorb the higher proportion of variance in the data matrix, they are no dimensional indicators of gradients

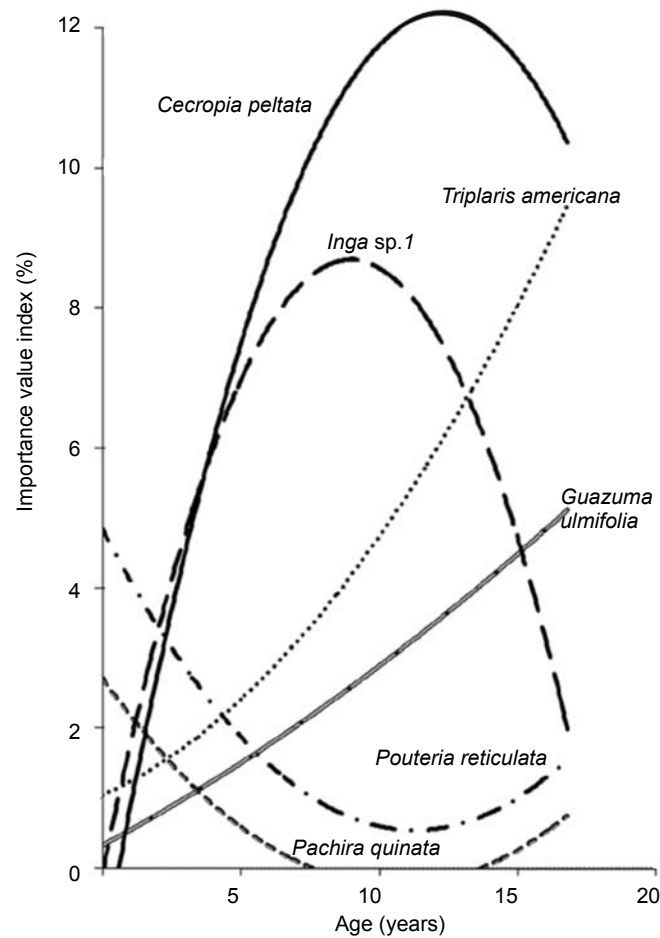


Figure 3 Development of key species based on the importance value index in high impact plots

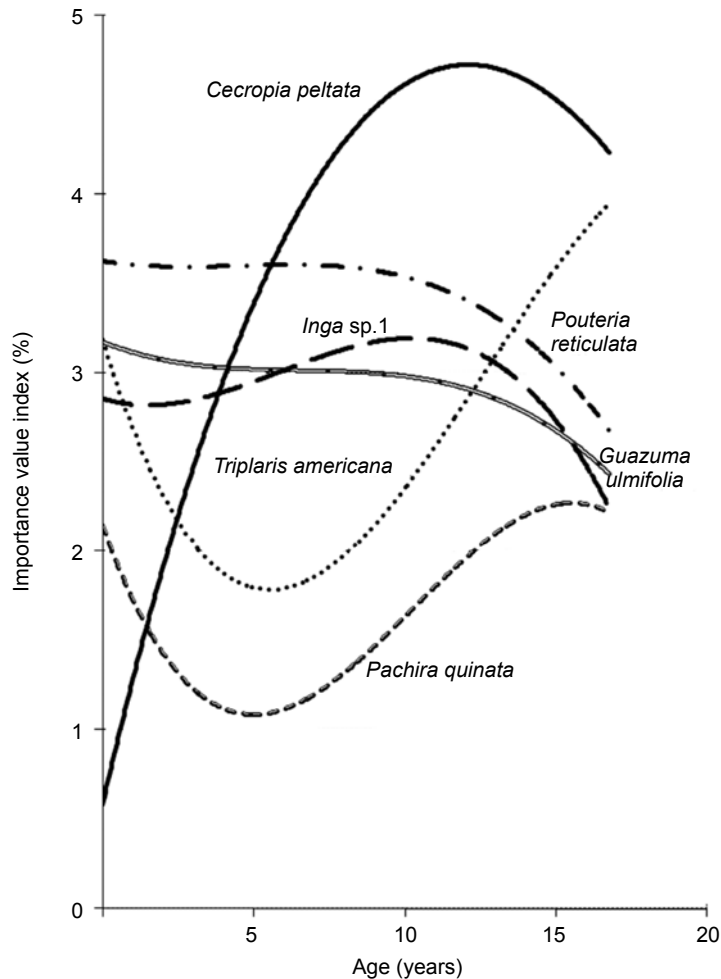


Figure 4 Development of key species based on the importance value index in medium impact plots

were rare in the unlogged forest. However, in medium and high impact areas, this group of species increased its basal area considerably. Some of these species declined after 12 years (Figures 3 and 4), but other pioneers replaced them.

The low impact plots showed tendency to recover its basal area, 16 years after perturbation. The plots with medium and high impact were slightly below the level prior to logging. However, with the rate of recovery observed, they may reach this level quickly.

DISCUSSION

We found early pioneer species such as *O. pyramidale* and *Inga sp. 1* which favoured high light level but had short lifespans. High disturbance level supported *C. peltata*, *G. ulmifolia* and *T. americana*, but they had longer lifespans. These results were in agreement with those of Kammesheidt (2000).

Slow growth nomad species associated with non-disturbance were *P. quinata*, *P. reticulata*, *S. leptopetala*, *C. thaisiana* and *S. sancona*. They were not favoured by open light conditions in their first development stages, but when they reached maturity they used gap light and were able to reach the canopy level.

Some species were related with no perturbation conditions but showed an increase with time. They were *S. terniflora*, *F. insipida*, *I. marginata* and *L. seemannii*. Natural gaps might favour these species in more advanced succession as shown in nomad species.

Ochroma, *Cecropia*, *Inga* and *Guazuma* are taxa mentioned as pioneer and related to secondary forests (Guariguata & Ostertag 2001, Drew et al. 2009, Castro-Luna et al. 2011). *Triplaris* is found in disturbed areas and small gaps, probably due to its slender crown. However, its macro leaves allow it to thrive in the low light flux inside the forest (Kammesheidt 2000).

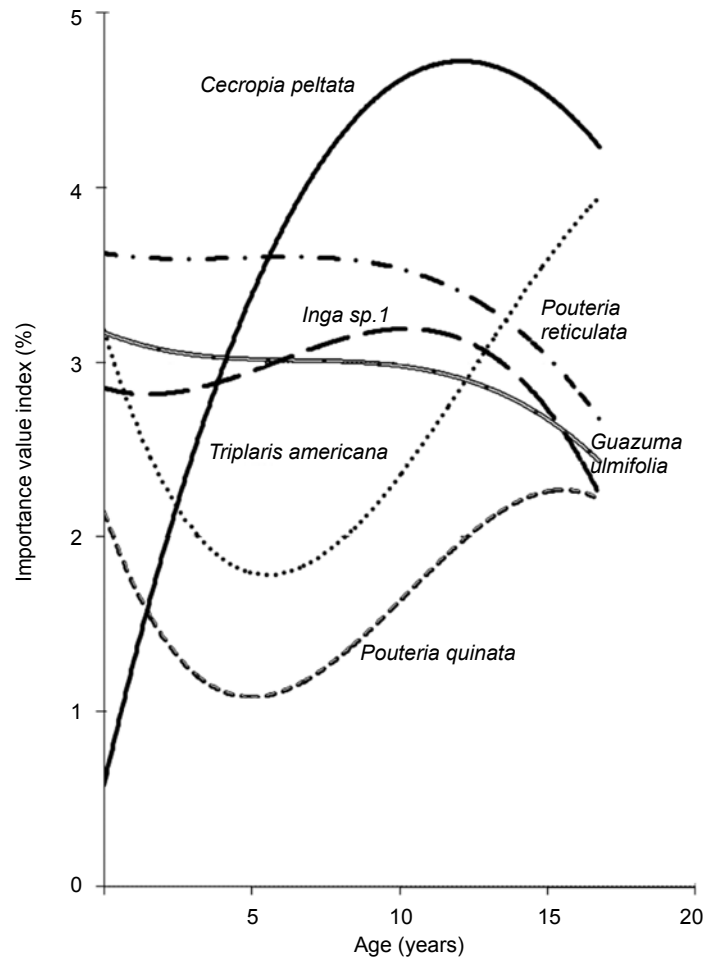


Figure 5 Development of key species based on the importance value index in low impact plots

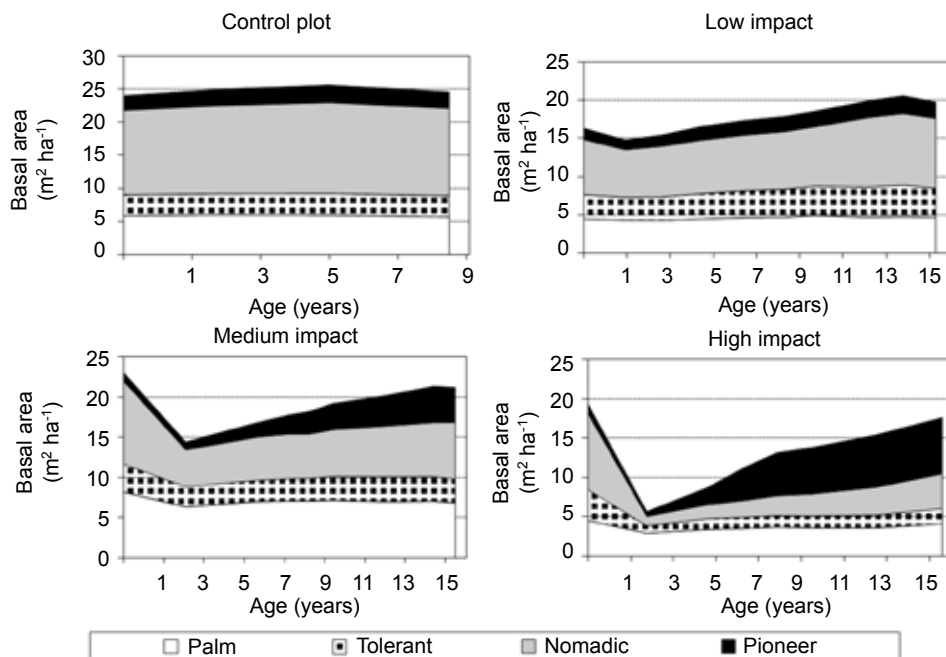


Figure 6 Forest recovery (basal area) at different logging intensities according to the ecological behaviour of species

Our research found that 12 years after disturbance early pioneer species declined in importance. Species such as *Cecropia leucocoma*, *Cecropia sciadophylla* and *Inga* sp. reached their highest abundance five to seven years after logging and at 21 years exhibited a drastic reduction but still maintained high share in basal area (De Oliveira 2005).

Pouteria reticulata and *P. quinata* were classified as late successional species (Tyree et al. 1998, Kammesheidt 2000) and were predominantly found in mature forests (Plonczak 1993, Ramírez 1995). Due to forest loss and very intensive logging, *Pouteria quinata* was considered vulnerable, which meant that it had high extinction risk in the medium term (Llamozas et al. 2003, Arends et al. 2005). Recovery of non-pioneer species, e.g. *Couroupita guianensis* and *Pouteria bilocularis*, had been regarded to be very slow after logging (De Oliveira 2005).

In abandoned agricultural areas, *C. peltata* and *G. ulmifolia* were found to be the species with the highest abundance during the first 19 years of succession (Gräfe 1981). *Inga* sp. and *T. americana* also increased their presence with intervention but in lower quantities.

Similar behaviour for each group of species covered in this study was observed by Plonczak (1993) and Kammesheidt (1994). In general, decline of *P. quinata* and increase of the pioneer species were observed.

It is important to highlight the similarities of all these results on the forest succession process. While the research work of later authors was carried out using chronosequences, the present study was based on direct observation in permanent plots. We will continue taking measurements in our plots. It allows us to know with more precision the life cycle of the early pioneers, the species of the following successional stage and the moment at which a significant takeover of characteristic climax species occurs.

The high impact level (60–80% basal area removed) appeared to be a very large loss of vegetation. However, several commercial species have a path distribution. Thus, in conventional logging, the high impact level does not seem strange in some restricted areas. Dekker and De Graaf (2003) considered the removal of 4 m² ha⁻¹ an unacceptably high level for sustainable forest management. Verburg and Van Eijk-Bos (2003) considered it low and moderate intensity the loss of 38 and 51% of

the original basal area. De Oliveira (2005) employed 17–25% in basal area reduction by the application of minimum cutting diameter from 45 to 55 cm in order to evaluate the effect of different logging intensities. Our high impact plots retrieved 90% of their original basal area in only 16 years (observation period). So it is not an unrecoverable disturbance to the forest.

A progressive succession was detectable 16 years after disturbance. The recovering stands were multilayered and had high cover forests (> 75% crown coverage; personal observation). The stands may show increasing similarity to old-growth forest functions in terms of recovery of soil nutrients and microclimatic conditions, water flow regulation, erosion reduction, capability to serve as carbon sink and wild life habitat (Guariguata & Ostertag 2001, Chinea & Helmer 2003).

High and medium impact stands showed basal area recovery of 90% in 16 years (Figure 6). This is slightly faster than in other neotropical logged sites: 96% in 21 years (De Oliveira 2005) or 98% in 20 years (Azevedo et al. 2008). Low impact and control plots presented basal area higher than former values (before treatments). Possibly, these forests were logged before 1961 (Kammesheidt et al. 2001b) and they were still growing up to their maximum basal area close to 22 m² ha⁻¹.

Nomadic species are very important because they are individuals of large size, attaining canopy level. Tolerant species are scarce since they are generally individuals of small size and do not reach the canopy. Pioneer species were present in the earlier forest (first measurement) probably due to the occurrence of small natural gaps.

Findings of *P. quinata* may have adverse long-term implications. Results showed that it was not favoured in early to medium successional stages. Regeneration depends on abundant seed trees and litter-free mineral soil (Kammesheidt et al. 2001b). Both conditions are not found in logged forests.

Our results indicated that prescribed logging cycles of 30-year interval should be longer to give time for the rehabilitation of commercial climax species (e.g. *P. reticulata* and *P. quinata*). Kammesheidt et al. (2001a) found through modelling that only 60-year cutting cycles provided sustainable yields. Furthermore, reduced-impact logging operations and silvicultural methods should be applied, especially on native commercial

species, e.g. shelterwood system and enrichment planting (Kammesheidt et al. 2001b).

CONCLUSIONS

Light-demanding species such as *C. peltata* and *Inga* sp. 1 achieved the highest IVI at about 12 years after disturbance, at a time when they showed a tendency to decline. The next successional stage would be dominated by other secondary species such as *T. americana* and *G. ulmifolia*. *Pouteria reticulata* and *P. quinata* were not favoured in the early successional stages. Undoubtedly, the forest recovered its basal area in a relatively short time (16 years), though the floristic composition differed considerably from old-growth forests. Therefore, it is necessary to extend the logging cycle to 60 years or longer and apply silvicultural treatments to support commercial species. The results could be used to recommend species for planting in wildlife corridors. These strips should improve riparian ecosystems and connect some of the abundant remnant stands at the Caparo Forest Reserve.

ACKNOWLEDGEMENTS

Financial support was provided by Consejo de Desarrollo Científico y Humanístico, Universidad de Los Andes (Project # FO-673-08-01-B). Special thanks to the personnel of the Caparo Experimental Station for their assistance during the fieldwork. We express gratitude to L Kammesheidt and M Guariguata for constructive comments on the manuscript.

REFERENCES

- ADLER G. 2002. La regulación de las poblaciones de mamíferos. Pp 329–343 in Guariguata M & Kattan G (eds) *Ecología y Conservación de Bosques Neotropicales*. Libro Universitario Regional, Costa Rica.
- ARENDS E, SÁNCHEZ D, VILLARREAL A, SERRANO J & BENÍTEZ M. 2005. Bosque Universitario El Caimital y la Estación Silvicultural El Manguito: dos lotes boscosos de los llanos occidentales para la conservación in situ de especies en peligro. *Revista Forestal Latinoamericana* 38: 1–19.
- AZEVEDO C DE, SANQUETTA C, MACEDO J & MACHADO S. 2008. Efeito de diferentes níveis de exploração e de tratamentos silviculturais sobre a dinâmica da floresta remanescente. *Floresta* 38: 277–293.
- BONTEMPS S, DEFOURNY P & VAN BOGAERT E. 2010. *GLOBCOVER 2009—Products Description and Validation Report*. European Space Agency (ESA) and The Université Catholique de Louvain, Belgium.
- TER BRAAK C. 1987. The analysis of vegetation–environment relationships by Canonical Correspondence Analysis. *Vegetatio* 69: 69–77.
- TER BRAAK C & VERDONSCHOT P. 1995. Canonical Correspondence Analysis and related multivariate methods in aquatic ecology. *Aquatic Science* 57: 255–289.
- CASTRO-LUNA A, CASTILLO-CAMPOS G & SOSA V. 2011. Effects of selective logging and shifting cultivation on the structure and diversity of a tropical evergreen forest in south-eastern Mexico. *Journal of Tropical Forest Science* 23: 17–34.
- CHINEA D & HELMER E. 2003. Diversity and composition of tropical secondary forests recovering from large-scale clearing: results from the 1990 inventory in Puerto Rico. *Forest Ecology and Management* 180: 227–240.
- CURTIS J & MCINTOSH R. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32: 476–496.
- DE GRAAF N. 2000. Reduced impact logging as part of domestication of neotropical rain forest. *International Forest Review* 2: 40–44.
- DEKKER M & DE GRAAF N. 2003. Pioneer and climax tree regeneration following selective logging with silviculture in Suriname. *Forest Ecology and Management* 172: 183–190.
- DE OLIVEIRA L. 2005. Efeito da exploração da madeira e de diferentes intensidades de desbastes sobre a dinâmica da vegetação de uma área de 156 ha na Floresta Nacional do Tapajós. PhD thesis, Universidade de São Paulo, Sao Paulo.
- DREW A, BOLEY J, ZHAO Y, JOHNSTON M & WADSWORTH F. 2009. Sixty-two years of change in subtropical wet forest structure and composition at El Verde, Puerto Rico. *Interciencia* 34: 34–40.
- FAO. 2011. *State of the World's Forests*. Food and Agriculture Organization of the United Nations, Rome.
- GRÄFE W. 1981. Estructura y dinámica de bosques secundarios jóvenes en los Llanos Occidentales de Venezuela. PhD thesis, Georg-August-Universität Göttingen, Göttingen.
- GUARIGUATA M & OSTERTAG R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148: 185–206.
- GUEVARA J. 2001. Recursos fitogenéticos y relaciones florísticas de la flórmula arbórea de las comunidades Forestales en la Estación Experimental Caparo, Estado Barinas. MSc thesis, Universidad Central de Venezuela, Maracay.
- JOHNS A. 1988. Effects of selective timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica* 20: 31–37.
- JOHNS J, BARRETO P & UHL C. 1996. Logging damage during planned and unplanned logging operations in the eastern Amazon. *Forest Ecology and Management* 89: 59–77.
- JURGENSON O. 1994. *Mapa de Vegetación y Uso Actual del Área Experimental de la Reserva Forestal de Caparo, Estado Barinas*. ULA-MARNR No 22. Universidad de Los Andes Cuaderno del Comodato, Mérida.
- KAMMESHEIDT L. 1994. Estructura y diversidad en bosques explotados de los llanos venezolanos occidentales

- considerando algunas características autoecológicas de las especies más importantes. PhD thesis, Georg-August-Universität Göttingen, Göttingen.
- KAMMESHEIDT L. 1998. Stand structure and spatial pattern of commercial species in logged and unlogged Venezuelan forest. *Forest Ecology and Management* 109: 163–174.
- KAMMESHEIDT L. 2000. Some autecological characteristics of early to late successional tree species in Venezuela. *Acta Oecologica* 21: 37–48.
- KAMMESHEIDT L, KÖHLER P & HUTH A. 2001a. Sustainable timber harvesting in Venezuela: a modelling approach. *Journal of Applied Ecology* 38: 756–770.
- KAMMESHEIDT L, TORRES A, FRANCO W & PLONCZAK M. 2001b. History of logging and silvicultural treatments in the western Venezuelan plain forests and the prospect for sustainable forest management. *Forest Ecology and Management* 148: 1–20.
- LLAMOZAS S, DUNO R, MEIER W, RIINA R, STAUFFER F, AYMARD G, HUBER O & ORTIZ R. 2003. *Libro Rojo de la Flora Venezolana*. Fundación Instituto Botánico de Venezuela, Caracas.
- LOZADA J. 2007. Situación actual y perspectivas del manejo de recursos forestales en Venezuela. *Revista Forestal Venezolana* 51: 195–218.
- LOZADA J & ARENDS E. 2000. Impacto de diferentes intensidades de aprovechamiento forestal sobre la masa remanente, en la Estación Experimental Caparo. *Revista Forestal Venezolana* 44: 73–80.
- LOZADA J, GUEVARA J, SORIANO P & COSTA M. 2006. Estructura y composición florística de comunidades secundarias en patios de rolas abandonados, Estación Experimental Caparo, Barinas, Venezuela. *Interciencia* 31: 828–835.
- MAGNUSSON W, DE LIMA O, REIS F, HIGUCHI N & FERREIRA J. 1999. Logging activity and tree regeneration in an Amazonian forest. *Forest Ecology and Management* 113: 67–74.
- MORET A, VALERA L, MORA A, GARAY V, JEREZ M, PLONCZAK M, RAMÍREZ N & HERNÁNDEZ D. 2008. Estructura horizontal y vertical de *Pachira quinata* (Jacq.) W.S. Alverson (Bombacaceae), en el Bosque Universitario “El Caimital”, Barinas, Venezuela. *Ecotrópicos* 21: 62–74.
- OCHOA J. 1997. Sensibilidades potenciales de una comunidad de mamíferos en un bosque productor de maderas de la Guayana Venezolana. *Interciencia* 22: 112–122.
- PLONCZAK M. 1993. *Estructura y Dinámica de Desarrollo de Bosques Naturales Manejados Bajo la Modalidad de Concesiones en los Llanos Occidentales de Venezuela*. Instituto Forestal Latinoamericano, Mérida.
- PLUMPTRE A. 1996. Changes following 60 years of selective timber harvesting in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management* 89: 101–113.
- QUESADA M, SANCHEZ G, ALVAREZ M, STONER K, AVILA L, CALVO J, CASTILLO A, ESPÍRITO-SANTO M, FAGUNDES M, FERNANDES G, GAMONB J, LOPEZARAIZA M, LAWRENCE D, CERDEIRA L, POWERS J, NEVES F, ROSAS V, SAYAGO R & SANCHEZ G. 2009. Succession and management of tropical dry forests in the Americas: review and new perspectives. *Forest Ecology and Management* 258: 1014–1024.
- RAMÍREZ H. 1995. Aplicación de un modelo de simulación de base individual a la dinámica del bosque tropical: un caso de los llanos venezolanos. MSc thesis, Universidad de Los Andes, Mérida.
- REDFORD K. 1992. The empty forest. *Bioscience* 42: 412–422.
- RUSCHEL A. 2008. *Dinâmica da Composição Florística e do Crescimento de uma Floresta Explorada há 18 Anos na Flona Tapajós, PA*. Documentos 341. Empresa Brasileira de Pesquisa Agropecuária, Belém.
- SCHARGEL R. 2005. Geomorfología y Suelos de los Llanos Venezolanos. Pp 57–113 in Hétier J & López R (eds) *Tierras Llaneras de Venezuela*. IRD, CIDIAT, UNELLEZ, Mérida.
- STONER K, LOBO J, QUESADA M, FUCHS E, HERRERÍAS Y, MUNGUÍA M, SALAZAR K, PALACIOS C & ROSAS V. 2007. Efecto de la perturbación del bosque en la tasa de visitas de murciélagos polinizadores y sus consecuencias sobre el éxito reproductivo y el sistema de apareamiento en árboles de la familia Bombacaceae. Pp 351–372 in Harvey C & Sáenz J (eds) *Evaluación y Conservación de Biodiversidad en Paisajes Fragmentados de Mesoamérica*. Inbio, Costa Rica.
- TYREE M, VELEZ V & DALLING J. 1998. Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes. *Oecologia* 114: 293–298.
- VERBURG R & VAN EIJK-BOS C. 2003. Effects of selective logging on tree diversity, composition and plant functional type patterns in a Bornean rain forest. *Journal of Vegetation Science* 14: 99–110.
- VERISSIMO A, BARRETO P, MATTOS M, TARIFA R & UHL C. 1992. Logging impacts and prospects for sustainable forest management in an old Amazonian frontier: the case of Paragominas. *Forest Ecology and Management* 55: 169–199.
- VINCENT L. 1970. Estudio sobre la tipificación del bosque con fines de manejo en la Unidad I de la Reserva Forestal de Caparo. MSc thesis, Universidad de los Andes, Mérida.

Appendix Total list and ecological behaviour for all evaluated species

Species	Ecological behaviour
<i>Albizia guachapele</i>	Nomadic
<i>Albizia niopoides</i>	Nomadic
<i>Allophylus racemosus</i>	Pioneer
<i>Annona montana</i>	Tolerant
<i>Annona</i> sp.	Tolerant
<i>Astronium graveolens</i>	Nomadic
<i>Attalea butyracea</i>	Palm
<i>Bactris major</i>	Palm
<i>Banara</i> sp.	Tolerant
<i>Bixa urucurana</i>	Tolerant
<i>Brosimum alicastrum</i> subsp. <i>bolivarense</i>	Nomadic
<i>Casearia nitida</i>	Tolerant
<i>Cassia grandis</i>	Not defined
<i>Cecropia peltata</i>	Pioneer
<i>Cedrela odorata</i>	Nomadic
<i>Ceiba pentandra</i>	Nomadic
<i>Cestrum latifolium</i>	Pioneer
<i>Chrysophyllum auratum</i>	Pioneer
<i>Chrysophyllum caracasenum</i>	Tolerant
<i>Citharexylum poeppigii</i>	Tolerant
<i>Citharexylum venezuelense</i>	Pioneer
<i>Clarisia biflora</i>	Tolerant
<i>Clavija longifolia</i>	Not defined
<i>Coccoloba caracasana</i>	Pioneer
<i>Coccoloba padiformis</i>	Tolerant
<i>Coccoloba</i> sp.	Not defined
<i>Cochlospermum vitifolium</i>	Pioneer
<i>Cordia collococca</i>	Nomadic
<i>Cordia thaisiana</i>	Tolerant
<i>Couroupita guianensis</i>	Tolerant
<i>Coussapoa villosa</i>	Nomadic
<i>Crateva tapia</i>	Nomadic
<i>Cupania americana</i>	Pioneer
<i>Dendropanax arboreum</i>	Tolerant
<i>Erythrina fusca</i>	Pioneer
<i>Erythroxylum</i> sp.	Pioneer
<i>Ficus insipida</i> subsp. <i>insipida</i>	Nomadic
<i>Ficus obtusifolia</i>	Not defined
<i>Fissicalyx fendlerii</i>	Nomadic
<i>Genipa americana</i> var. <i>caruto</i>	Not defined
<i>Goethalsia</i> sp.	Tolerant
<i>Guapira olffersiana</i>	Pioneer
<i>Guarea guidonia</i>	Nomadic
<i>Guazuma ulmifolia</i>	Pioneer
<i>Hamelia patens</i>	Not defined
<i>Heliocarpus americanus</i>	Pioneer
<i>Hirtella</i> sp.	Pioneer
<i>Inga marginata</i>	Nomadic
<i>Inga oerstediana</i>	Pioneer

(continued)

Appendix (continued)

Species	Ecological behaviour
<i>Inga</i> sp 1.	Pioneer
<i>Inga</i> sp 2.	Tolerant
<i>Inga</i> sp 3.	Not defined
<i>Inga</i> sp 7.	Not defined
<i>Licania apetala</i> var. <i>aperta</i>	Nomadic
<i>Lonchocarpus pictus</i>	Tolerant
<i>Lonchocarpus sericeus</i>	Not defined
<i>Lonchocarpus</i> sp.	Not defined
<i>Luehea seemannii</i>	Nomadic
<i>Maclura tinctoria</i>	Not defined
<i>Mouriri barinensis</i>	Tolerant
<i>Myrcia</i> sp.	Not defined
<i>Ochroma pyramidale</i>	Pioneer
<i>Ocotea</i> sp 1.	Tolerant
<i>Ocotea</i> sp2.	Not defined
<i>Pachira quinata</i>	Nomadic
<i>Piper</i> sp.	Pioneer
<i>Piptadenia</i> sp.	Not defined
<i>Platymiscium pinnatum</i>	Nomadic
<i>Platymiscium polystachyum</i>	Not defined
<i>Pouteria reticulata</i>	Nomadic
<i>Protium crenatum</i>	Tolerant
<i>Psychotria carthagenensis</i>	Not defined
<i>Pterocarpus acapulcensis</i>	Nomadic
<i>Roystonea oleracea</i>	Palm
<i>Sapium aubletianum</i>	Nomadic
<i>Senna alata</i>	Pioneer
<i>Senna</i> sp.	Not defined
<i>Sloanea terniflora</i>	Nomadic
<i>Spondias mombin</i>	Nomadic
<i>Sterculia apetala</i>	Not defined
<i>Stylogyne venezuelana</i>	Not defined
<i>Swartzia leptopetala</i>	Nomadic
<i>Swietenia macrophylla</i>	Nomadic
<i>Syagrus sancona</i>	Palm
<i>Symmeria paniculata</i>	Nomadic
<i>Tabernaemontana cymosa</i>	Tolerant
<i>Terminalia oblonga</i>	Nomadic
<i>Trichanthera gigantea</i>	Pioneer
<i>Trichilia maynasiana</i>	Tolerant
<i>Trichilia pallida</i>	Not defined
<i>Trichilia trifolia</i>	Tolerant
<i>Trichilia trifolia</i> subsp.	Pioneer
<i>Triplaris americana</i>	Pioneer
<i>Urea caracasana</i>	Pioneer
<i>Vitex orinocensis</i> var. <i>multiflora</i>	Nomadic
<i>Zanthoxylum caribaeum</i>	Pioneer
<i>Zanthoxylum culantrillo</i>	Pioneer
<i>Ziziphus saeri</i>	Not defined