Research paper

Is it possible that the structure of tropical rainforests has recovered 40 years after clear-cutting?

Luz Amalia Forero-Peña[1], Edna Ivonne Leiva-Rojas[2*] and Ramiro Ramírez-Pisco[3]

Forero-Peña, L.A., Leiva-Rojas, E.I., Ramírez-Pisco, R. 2022. Is it possible that the structure of tropical rainforests has recovered 40 years after clear-cutting? – Forestry Studies | Metsanduslikud Uurimused 76, 64–75, ISSN 1406-9954. Journal homepage: http://mi.emu.ee/forestry.studies

Abstract. The tropical rainforest of Bajo Calima, Buenaventura, Colombia, was known for its large biodiversity and enormous regeneration potential. During the 1970–90s, industrial use through clear-cutting gave rise to secondary forest (SF), which is now a collective property of the communities that inhabit it. The productivity of secondary forest would recover after 30 years according to the linear recovery trend, as predicted by Mazuera (1985). The purpose of conducting this research in Bajo Calima, Colombia was to quantify the productivity of SF at different ages after clear-cutting. Plots of 0.1 ha were selected after 23, 27, 31 and 35 years of SF following clear-cutting of the initial primary forest (PF). It is now managed through selective logging. Samples of equal size of PF and SF without selective logging, called mature secondary forest MSF (> 40 years), were used as controls. The productivity variables of the SF expressed as basal area, volume (Vol) and aerial biomass (AB), on average for the four ages studied was 45%, 29% and 22% compared to the productivity of the PF, and 94%, 50% and 49% with respect to the productivity of the MSF. Without the opportunity to reach maturity the trend predicted by the recovery model was not achieved and the SF showed productive characteristics far below those of the initial primary forest.

Key words: chronosequence, structure, tropical secondary forest, productive variables.

Authors' addresses: [1]Facultad de Ingeniería Forestal, Universidad del Tolima, Barrio Santa Helena Parte Alta Cl 42 1-02, 730006299 Ibagué, Tolima, Colombia; [2]Facultad de Ciencias Agrarias. Universidad Nacional de Colombia, Carrera 65 Nro. 59A-110, 050034 Medellín, Colombia; [3]Facultad de Ciencias. Universidad Nacional de Colombia, Carrera 65 Nro. 59A-110, 050034 Medellín, Colombia; *e-mail: eileiva@unal.edu.co

Introduction

The definition of secondary forest (SF) in general refers to forests that regenerate naturally in deforested areas as a result of succession following logging or subsequent change in land use (Ngo Bieng *et al.*, 2021; Brown & Lugo, 1990). SF corresponds to forest ecosystems developed after the destruction of the original or primary forest (PF) caused by natural and human disturbances (CNCF, 1999), giving rise to the repopulation process (Finegan, 1997) which is also termed forest recovery (Emrich *et al.*, 2000). Different concepts agree that SF is developed mostly without human intervention (Emrich *et al.*, 2000). According to Ngo Bieng *et al.* (2022), more than a half of the world's tropical forests are naturally regenerating forests: second-

DOI: 10.2478/fsmu-2022-0004

© 2022 by the authors. Licensee Estonian University of Life Sciences, Tartu, Estonia. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).

ary and degraded. Currently it refers to degraded secondary forests (SDF) that are growing in areas that have suffered from unsustainable human activities, including former deforestation.

New vegetation cover has characteristics within the regeneration process: it is considered that the process follows stages that are successive in time. The successions are dynamic and tend to a state of equilibrium or climax, commonly known as SF, with characteristics similar to the original forest. The different successional stages differ in their floristic composition and structure, with common components and processes they can be grouped and studied as an association.

SF dynamics can be affected by natural disturbances, such as fire, pests, diseases, floods, and by deforestation. It has been described that the first successional stages in the SF are highly vulnerable to change in land use, meaning a loss of some soil or vegetational attributes – such as the floristic composition and structure (Guariguata & Ostertag, 2002) – will negatively influence its operation leading to a possible decrease in productive capacity.

In Bajo Calima, 35,270 hectares were logged between 1960 and 1990 and 23,600 hectares of primary forest (PF) were preserved by the forestry concession (Rodríguez, 1989). Between 1985 and 1991, the structure and diversity at early ages of natural regeneration after clear-cutting in these forests were determined (Ladrach & Mazuera, 1985; Faber-Langendoen, 1992; Forero-Peña & Ordóñez, 1992; Faber-Langendoen & Gentry, 1991). Regarding the rotation time, Mazuera (1985) set a period of 30 years for the SF to equalize the basal area of the PF. Faber-Langendoen (1992) warned that biomass could decline between 15 and 30 years due to the natural death of many pioneer species. Furthermore, Wright (1997) reported that most SFs were being used, to some extent, by settlers. Recently the study carried out by Pacheco-Pascagaza (2020) found that between 2007 and 2018, 33.75% of the forest was significantly modified with an intensity of 4,207 ha per year, almost 10% of the area was deforested and only 2.4% was regenerated.

Currently most of the forests in the study have been exploited with this continuing. In Bajo Calima harvesting is done selectively to extract timber and non-timber resources among other activities (Forero-Peña & Mora-Delgado, 2017). Martínez (2006) reported that the average cutting diameter in the same 35-year-old secondary forests was 10.2 cm at diameter breast height (DBH), and found 447 stumps ha^{-1} that had been cut down to be marketed as sticks (more than 6 m in length) and *tucas* (three meters or less in length).

In the forest, species show different growth patterns, some with a long life and slow growth, and others with a short life span – the latter are called pioneer species (Zent, 1995). Finegan (1997) points out that there are two strategies in the colonization stages; the first strategy sees species exhibit high reproductive intensity, whereas the second strategy favours species with better survival and competition capacities.

In Colombia, little work has been carried out regarding the disturbed SF regeneration dynamics, in which the production trends of the basal area (BA), volume (Vol), and biomass (B) are identified. Specifically, in the SF of Buenaventura approaches have focused on describing impacts, such as degradation and changes on floristic composition (Martínez, 2006). The objective of this research was focused on identifying changes in the SF structure and productive variables (BA, Vol, and B) in a chronosequence of 40 years in Bajo Calima, Colombia. The study of SF chronosequences allows a recognition of changes in landscape in the ecosystem, caused over time and are examined in periods to identify the succession (Peña-Claros, 2003).

Materials and Methods

Location of the Study Area

The study area is classified by the Holdridge system as transitional between tropical wet and tropical pluvial forest of the Chocó biogeographical region (IDEAM, 2008). It is in the Colombian Pacific lowlands, near Buenaventura (Figure 1) in territories of the black community from the lower basin of the Calima River. Its extension is 66,000 hectares, located at altitudes of 40 to 150 m, between the coordinates 3° 54′ – 4°06′ North Latitude and 76° 50′ – 77° 30′ West Longitude. The area has an average rainfall of 7,467 mm year^{-1}, the rainiest months are May, September, October and November with an annual average of 255 rainy days. The average temperature is 26°C and the relative humidity is 88%, the average sunshine is 2.5 hours light day^{-1}.

Sampling design

32 temporary sampling plots of 0.1 ha (10 m x 100 m) were established with random sampling. Six plots were selected for each age of SF: 23, 27, 31 and 35 years after clear-cutting; four in mature secondary forest MSF (> 40 years), and four in PF. The morphological inventory was carried out in each plot of different age. The variables measured were DBH in cm and height of trees (HT) in m. BA in m^2 ha^{-1}, density (D) number of trees ha^{-1}. The Vol (m^3 ha^{-1}) was estimated with the formula: *BA (m^2) x HT (m) x 0.5* for each 0.1 ha plot. The AGB in Mg ha^{-1} was estimated with the formulas reported by Faber-Langendoen (1992) for the different groups of species:

Ephemeral Heliophytes (Uhl & Jordan, 1984):

$$Dry\ Matter\ (g) = 0.134(DBH^2 \times H)+15.536$$

Durable Heliophytes (Uhl & Jordan, 1984):

$$Log_{10} Dry\ matter\ stems\ (kg) = 0.860\ Log_{10} (DBH^2 \times H)+0.2017$$

Partial and durable sciophytes (Buschbacher *et al.*, 1988):

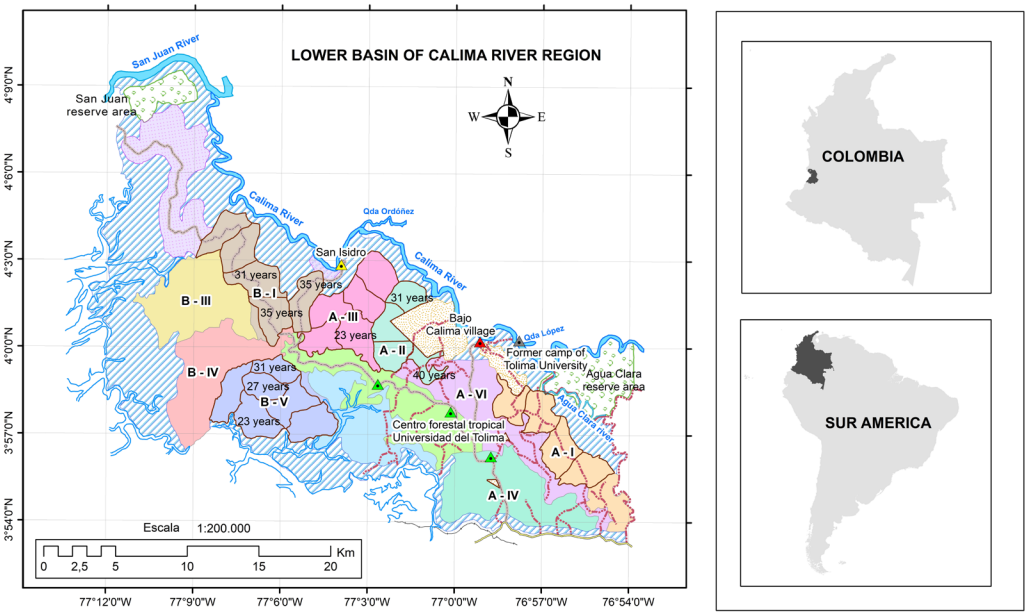


Figure 1. Bajo Calima Region, location of the sampling areas.

$$Ln\ Biomass\ (kg) = (0.9906)\ x\ Ln\ \{(DBH^2\ x\ H)\ x\ 0.603\} - 2.9678$$

Palmtrees (Buschbacher *et al.*, 1988):
Palmtrees without stipe:

$$Log_{10} Dry\ matter = 2.094\ (Log_{10} L_f) - 2.776$$

where L_f is the length of the leaves.
Palms with stipe:

$$Dry\ matter\ (g) = 0.0381\ (DBH^2\ x\ H)^{0.722}$$

Statistical analysis

The nested analysis of variance for each age and the multiple range comparison LSD (least significant distance) test were performed to determine the significance difference in vegetation between the chronosequence ages, using the Statgraphics® program. To analyze the amplitude of the changes in the horizontal structure of the forests, linear and polynomial regression models were applied.

Results

Horizontal structure and productivity of the forest

The trees in different plots of the chronosequence showed a similar DBH. There were significant differences with respect to the MSF and the PF, the latter with a DBH greater than 22 cm (Table 1). Tree density presented variations without a defined trend, the highest D was found in PF. There was a significant decrease in density in short periods, 27 to 31 and 31 to 35 years, in the same way as in Pernambuco, although these are dry forests (Melo *et al.*, 2019).

The tallest trees were found in MSF (>40 years), the lowest trees were in 27- and 31-year-old SF. 23- and 35-year-old PF did not show significant differences with SF. The BA (Table 1) was similar in evaluated ages of the SF. At the age of 27 years the lowest BA was obtained, but all the ages were significantly lower than PF, with low values corresponding to 50% of BA of PF (33.4 $m^2\ ha^{-1}$). BA did not present a continuous ascent as the forest age advanced, not showing a definite progression in this variable. In the regeneration process, the behavior was like that of Borneo (Hayward *et al.*, 2021), D and BA without significant differences between the ages after being logged.

The BA in Bajo Calima, after 23 years of logging, reached 15.8 $m^2\ ha^{-1}$ and 15.9 $m^2\ ha^{-1}$ at 40 years, with lower quantity at 31 and 35 years, but without significant differences. The linear regression of the BA over time was not significant (P val-

Table 1. Structure and productivity of the secondary forest (SF) at different ages after clear-cutting MSF (>40 years) and a primary forest (PF) in Buenaventura, Colombia. Age: years after clear-cutting. DBH: diameter breast height. HT: height total. D: diameter. BA: basal area. Vol: volume. AGB: above-ground biomass.

Age (years)	DBH (cm)	HT (m)	D (Tree ha^{-1})	BA ($m^2 ha^{-1}$)	Vol ($m^3 ha^{-1}$)	AGB (Mg)
23	15.0 a*	10.6 b	790 b	15.8 b	93.9 cb	56.5 b
27	15.0 a	8.3 a	553 a	11.1 a	46.6 a	27.3 a
31	15.3 a	9.6 a	720 b	14.8 b	78.7 b	52.3 b
35	15.9 a	11.7 b	624 b	14.4 b	87.8 b	54.1 b
>40	17.5 b	19.3 c	548 a	15.9 b	174.5 d	110.9 c
PF	22.7 c	12.8 b	853 c	33.4 c	294.6 e	242.2 d

* Different letters within each column represent significant differences in the LSD test.

ues>0.05, R^2<0.5). Tests made with other models were not significant either (R^2 values <0.5); the age of the SF is not adequate to predict the BA.

The wood volume of the SF (Table 1) presented significant differences between the years elapsed after the intervention with no sequential trend and significantly less than the MSF (>40) and the PF, which was the highest (Table 1). The estimation of volume in relation to age (Figure 2) was significant and corresponded to a polynomial model (R^2=0.74):

$$\text{Vol } (m^3 ha^{-1}) = 767.41 - 51.044 \text{ age (years)} + 0.9154 \text{ age}^2 \text{ (years)}.$$

The AGB did not show significant differences between ages of the SF after logging, its accumulation being similar – except for that of 27 years where it was significantly lower (Figure 3). Furthermore, the AGB was significantly higher in the PF and showed differences compared to the RSF and the disturbed (Aide *et al.*, 2013).

The homogeneity of the different variables with respect to age of the SF can be explained with the diametric distribution. When analyzing each set of ages, a similar repeating pattern of structure is found at different ages of stands (Figure 4), where most trees are located in the diametric class I (10–15 cm), the second largest group is made up of class II (15–20 cm), these two classes exceed 60%. It was found that the tree population has small diameters despite the age (SF greater than 23 years), few trees – less than 20% – are large, with DBH greater than 30 cm.

The 23-, 27- and 31-year series have a similar distribution, with an equivalent number of trees in each diameter class. It is noteworthy that even after eight years there were no significant changes in the evolution of the forest, probably due to selective logging by the inhabitants of the SF.

Relationship between forest age and production variables and predictions

The forest in the chronosequence studied did not present a significant relationship between the production and age variables (P<0.05). However, Faber-Langendoen (1992) reported a significant ratio during the early stages of the succession in the same forests, finding a progressive dynamic, which was not evidenced in this study 20 years later. Furthermore, the BA corresponded to what was found by this author for a SF with 18 years of evolution.

Faber-Langendoen (1992) showed that after twelve years, the BA and the AGB had recovered by 46% and 37%, respectively, where 63% of this AGB was mainly attributable to pioneer species, indicating an early forest succession. An extrapolation of their model beyond twelve years of clear-cutting suggested that the AB would

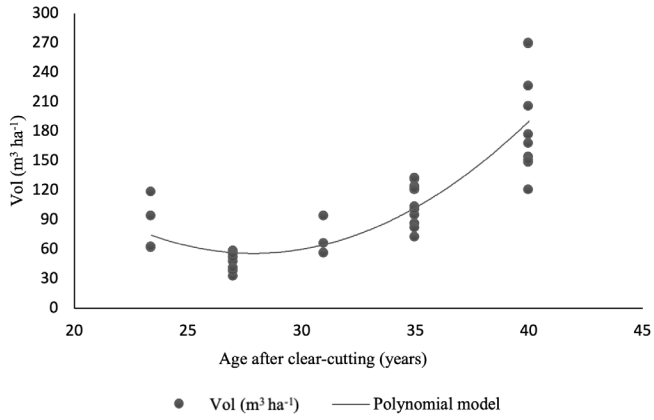


Figure 2.

Ratio between volume (Vol $m^3 ha^{-1}$) of the secondary forest (SF) and age after clearcutting (trees with DBH>10 cm) in Bajo Calima, Buenaventura, Colombia.

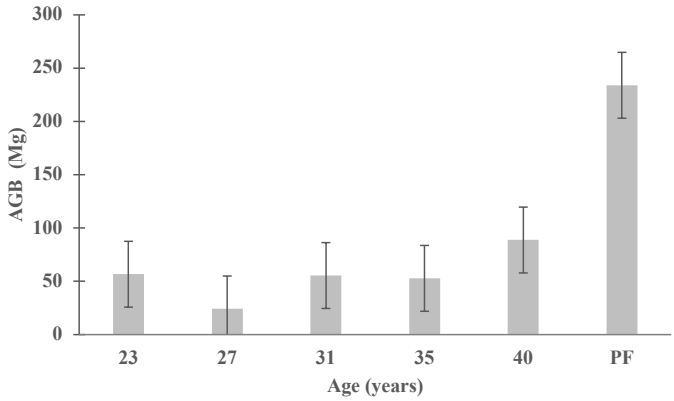


Figure 3.

Accumulation of above-ground biomass (AGB) in the secondary forest (SF) at four ages after clear-cutting (Trees with DBH>10 cm) in a mature secondary forest MSF (>40-year-old) and in a PF in Bajo Calima, Buenaventura, Colombia.

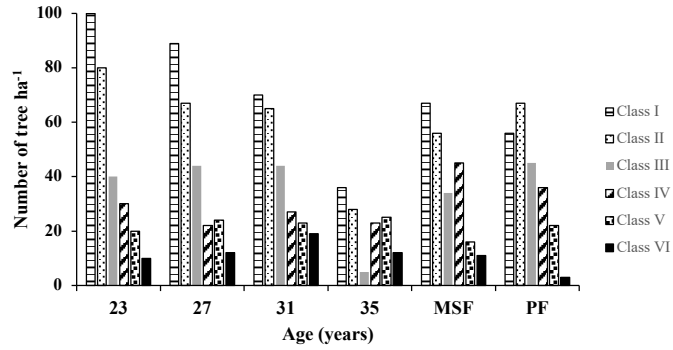


Figure 4.

Distribution of the number of trees (D) by diameter class (DBH>10 cm, all species) in each age of the secondary forest (SF), mature secondary forest (MSF) and primary forest (PF). Class I: 10–15 cm, Class II: 16–20 cm, Class III: 21–25 cm, Class IV: 26–30 cm, Class V: 31–35 cm, Class VI: >35 cm.

equal the mature forest in 30 years, a period that would be set as "rotation time" (Ladrach & Mazuera, 1985). However, it was warned that it would be an unrealistic model since biomass could decline between 15 and 30 years due to the death of many pioneers (Faber-Langendoen, 1992). With our results, the productive decline of the forest is confirmed due to not previously considered causes, such as anthropogenic causes, in addition to the natural ones proposed by them. Also, the generality reported in research on successionally with significant differences between ages is distorted until reaching stages with characteristics similar to a PF with respect to production variables.

It is evident that the selective harvesting system carried out by the communities residing in the forest impaired the growth dynamics to such an extent that the extraction of products (wood) exceeds that of replacement (regeneration), limiting the resilience of the forest (Forero-Peña *et al.*, 2020). These results agree with what was reported by Valencia *et al.* (2004) who verified in the Ecuadorian Amazon how the localized use alters the diametric distribution, modifies the behavior "in situ" of environmental variables, such as radiation, temperature and therefore the microclimate, bringing as a consequence the alteration of succession course and vegetation growth, which would partially explain what happened in Bajo Calima.

Discussion

The chronosequence of the rain tropical SF did not represent a successional dynamic, since the magnitude of changes of the variables BA, Vol and AGB was not significant. Changes have presented without a defined trend during the 40 years evaluated. Al-

though, at the age of 27, a lower productivity and tree D were evident, attributable to the frequency of anthropogenic interventions, the rate of recovery becomes uncertain because they have been affected by human activity at different levels (Norden *et al.*, 2009) and it is possible that the extractions were of such magnitude that affect the retrieval of D and BA (Forero-Peña *et al.*, 2020), which differs from what was found in the Brazilian Amazon where 80% of BA is achieved in 30 years (de Avila *et al.*, 2015).

It was shown that the production values, similar between three ages: 23, 31 and 35, do not represent the productivity they had in the past. The BA of the 31-year-old SF is similar to that of the younger forests, 18 and 20 years (De las Salas, 2002; Faber-Langendoen, 1992; Forero-Peña & Ordóñez, 1992; Mazuera, 1985), and is lower, that other tropical forest in equivalent conditions (Finegan & Sabogal, 1988), in Nicaragua (Ferreira *et al.*, 2002) and Puerto Rico (Aide *et al.*, 1996).

The BA in Bajo Calima, after 23 years of logging, reached 15.8 m^2 ha^{-1} and 15.9 m^2 ha^{-1} at 40 years, values that deviate to a great extent from that reported by Peña-Claros (2003) for Bolivian Amazon forests due to clear-cuttings for agriculture, which after two years of abandonment presented a 12.3 m^2 ha^{-1} and at 40 years 36.3 m^2 ha^{-1}, doubling in this case the BA of Bajo Calima.

There were no differences between SF of 23, 31, and 35 years, but the chronosequence showed highly significant differences between the SF of 23, 31 and 35 years old and the PF of Bajo Calima. In this disturbed group, the BA, Vol and AGB corresponded to 45%, 29% and 22% with respect to the PF, and 94%, 50% and 49% with respect to MSF without intervention. While in Bolivia it was reported that at 25 years the SF reached 70% of the mature forest BA (Finegan & Sabogal, 1988), and in the Amazon 80% of the BA after 30 years (de Avila *et al.*, 2015). In Asian forests it took more time: in Indonesia to reach 82% AGB and 74% AGB took 55 years (Brearley *et al.*, 2004), and in Singapore after 56 years only 58% of the AGB of the neighbouring PF was recovered (Chua *et al.*, 2013) showing that the recovery of the forest structure is slow in these areas.

Poorter *et al.* (2021) analyzed 12 attributes during the secondary succession of abandoned and slightly disturbed tropical forests, concluding that they have the potential to regrow. After 20 years, the forest attributes reached 78% (33% to 100%) of their old growth values, the recovery to 90% of the old growth values for the structure and diversity of species was from 2.5 to 6 decades, while for the biomass and the composition of species it was slower (>12 decades). Particularly, Zambiazi *et al.* (2021) found that in some SF located in the Brazilian Atlantic, abandoned from migratory agriculture, and probably not intervened, they managed to accumulate more volume of wood in fast-growing species.

The characterization of PF in Bajo Calima (Rodríguez, 1989) reported an AGB of 190.7 Mg ha^{-1} (vegetation greater than or equal to 3 cm in diameter), considerably less than that of the PF studied, even more so because this measurement only took into account those with a diameter greater than 10 cm.

As for the results of the AGB of this research, they contrast with those reported by Saldarriaga *et al.* (1988) in a SF in the Alto Río Negro basin of the Colombian-Venezuelan Amazon, where they reported linear increases up to 40 years, similar to the values reported in SF in Puerto Rico (Aide *et al.*, 1996) and Nicaragua (Ferreira *et al.*, 2002), where production and density increased with the age of SF. In Chocó, Colombia, under extremely high rainfall, production also increased after just 10 years (Quinto Mosquera & Moreno Hurtado, 2011).

The evolution of the SF after 23 and up to 35 years after clear-cutting does not show significant changes in BA, Vol, and AGB variables, which are the basis of the

forest recovery or resilience indicators. It is noteworthy that in this rain tropical zone, there are no limitations due to precipitation, on the contrary rainfall exceeds 7,000 mm annual rainfall, with 255 days of rain per year. Under these conditions, the effect of water on the regenerative process of the forest was not evident, as proposed by Poorter *et al.* (2016) in their modeling study, considering available water as one of the favorable variables for the process.

The AGB of MSF was lower than PF, attributed to the death of many pioneer species. While the AGB accumulated at 23 years (56.5 Mg ha^{-1}) in the SF is lower than that of other tropical forests, in Costa Rica a 20-year-old SF accumulated 65 Mg ha^{-1} of AGB being in the range reported by Chacón *et al.* (2007) and Yan *et al.* (2006).

In tropical eastern Africa (Uganda) (Osazuwa-Peters *et al.*, 2015), as in Bajo Calima, neither the density nor the BA nor the biomass recovered after more than 40 years of logging, revealing the fragility of the tropical SF.

The homogeneity for the diametric distribution was at 23, 27 and 31 years; without successional changes, it seems that regeneration had been continuous (De Lima *et al.*, 2017). This distribution compared to that reported by Forero-Peña & Ordóñez (1992) is similar to that of a 20-year-old forest, but with fewer trees in each size class, a condition that coincides with that reported by Martínez (2006) for a 35-year-old SF subjected to exploitation and with that found by Vallejos (1996) for the Ecuadorian Amazon. Louman *et al.* (2001) affirms that young SF frequently correspond to approximately coetaneous structure, while the PF, intervened or not, as well as mature secondary ones, present disetaneous structure as is the case of the SF of this research, but with a small diameter.

In the Bajo Calima chronosequence, the resilient capacity of the SF is not evident in the dynamics of its biomass since it does not increase. It is reasoned that this is due to the harvesting carried out by local communities of trees that exceed 10 cm in diameter, affecting successional trajectories, leading to a deleterious effect on forest development (Aide *et al.*, 2013). Thus, recovery in this area is influenced by the context, idiosyncrasy (Martínez, 2006; Forero-Peña & Mora-Delgado, 2017; Norden *et al.*, 2015), the intensity of use (Martínez, 2006; Hüller *et al.*, 2011; Aguiar *et al.*, 2019), and partly by weather conditions.

Conclusions

The structure and productive variables in the SF, after clear-cutting with periods that go beyond 20 and up to 40 years present their own dynamics, which are affected by the inhabitants of the region, without a tendency to reach maturity and far from the productive characteristics of the preceding PF.

The magnitude of the changes of the different variables in the evaluated ages was not significant. In general, the structure of the SF at different ages shows a certain similarity. The results for the ages studied do not meet the characteristics of a sequence, the change is not ordered or unidirectional in progression.

In the secondary forests of Bajo Calima after clear-cutting, it was evident that the resilience process is conditioned to selective extraction, where the forest production variables do not present the same recovery trend.

Acknowledgements. We thank the students of the AgroXue team for their operative support. We are most grateful to all local participants and the Community Council of Bajo Calima (Comunidad y Consejo Comunitario del bajo Calima). We thank Wojciech Waliszewski for his writing assistance and reading the article (English manuscript). This work was supported by the Centro Forestal Tropical of the Universidad del Tolima and Grupo AgroXue de la Universidad Nacional de Colombia Sede Medellín.

References

Aguiar, S.H.S., Carvalho, J.O.P., Ruschel, A.R., Ramos, E.M.L.S, Rocha, E.S., Castro, T.C., Silva, B.M.F. 2019. Dynamics of natural regeneration of timber species during three decades after logging in the Tapajós National Forest, Brazil. (Dinâmica da regeneração natural de espécies madeireiras durante três décadas da exploração florestal na Floresta Nacional do Tapajós, Brasil). – Scientia Forestalis, 47(121), 157–166. (In Portuguese).

Aide, T.M., Clark, M.L., Grau, H.R., López-Carr, D., Levy, M.A., Redo, D. 2013. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). – Biotropica, 45(2), 262–271. https://doi.org/10.1111/j.1744-7429.2012.00908.x.

Aide, T.M., Zimmerman, J.K., Rosario, M., Marcano, H. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. – Biotropica, 28(4), 537–548.

Brearley, F.Q., Prajadinata, S., Kidd, P.S., Proctor, J., Suriantata. 2004. Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. – Forest Ecology and Management, 195(3), 385–397.

Brown, S., Lugo, A.E. 1990. Tropical secondary forests. – Journal of Tropical Ecology, 6, 1–32.

Buschbacher, R., Uhl, C., Serrão, E.A.S. 1988. Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. – Journal of Ecology, 76(3), 682–699. https://doi.org/10.2307/2260567.

Chacón, P., Leblanc, H.A., Russo, R.O. 2007. Carbon fixation in secondary forests of the humid tropical region of Costa Rica. (Fijación de carbono en bosques secundarios de la región tropical húmeda en Costa Rica). – Tierra Tropical, 3, 1–11. (In Spanish with English summary).

Chua, S.C., Ramage, B.S., Ngo, K.M., Potts, M.D., Lum, S.K.Y. 2013. Slow recovery of a secondary tropical forest in Southeast Asia. – Forest Ecology and Management, 308, 153–160. https://doi.org/10.1016/j.foreco.2013.07.053.

CNCF (Comisión Nacional de Certificación Forestal). 1999. Standards and procedures for sustainable management and forest certification in Costa Rica. (Estándares y procedimientos para el manejo sostenible y la certificación forestal en Costa Rica). San José, Costa Rica, CNCF. 54 pp. (In Spanish).

de Avila, A.L., Ruschel, A.R., de Carvalho, J.O.P., Mazzei, L., Silva, J.N.M., Lopes, J.C., Araujo, M.M., Dormann, C.F., Bauhus, J. 2015. Medium-term dynamics of tree species composition in response to silvicultural intervention intensities in a tropical rain forest. – Biological Conservation, 191, 577–586. http://dx.doi.org/10.1016/j.biocon.2015.08.004.

De Las Salas, G. 2002. The secondary forests of tropical America: prospects for their sustainable management. (Los bosques secundarios de América tropical: perspectivas para su manejo sostenible). – Bois et Forets des Tropiques, 272(2), 63–73. (In Spanish).

De Lima, R.B., Bufalino, L., Alves Junior, F.T., Silva, J.A.A., Ferreira, R.L.C. 2017. Diameter distribution in a Brazilian tropical dry forest domain: predictions for the stand and species. – Anais da Academia Brasileira de Ciências, 89(2), 1189–1203. https://doi.org/10.1590/0001-3765201720160331.

Emrich, A., Pokorny, B., Sepp, C. 2000. The significance of secondary forest management for development policy. TÖB Series No. FTWF-18e. Eschborn, Germany, GTZ. 198 pp.

Faber-Langendoen, D. 1992. Ecological constraints on rain forest management at Bajo Calima, western Colombia. – Forest Ecology and Management, 53(1–4), 213–244.

Faber-Langendoen, D., Gentry, A.H. 1991. The structure and diversity of rain forests at Bajo Calima, Chocó Region, western Colombia. – Biotropica, 23(1), 2–11.

Ferreira, C.M., Finegan, B., Kanninen, M., Delgado, L.D., Segura, M. 2002. Floristic composition and secondary forest structure in the San Carlos municipal district, Nicaragua. (Composición florística y estructura de bosques secundarios en el municipio de San Carlos, Nicaragua). – Revista Forestal Centroamericana, 38, 44–50. (In Spanish).

Finegan, B. 1997. English title. (Bases ecológicas para el manejo de bosques secundarios de las zonas húmedas del trópico americano; recuperación de la biodiversidad y producción sostenible de madera). – Elías, E. (ed.). Proceedings of the International Workshop on the current status and potential of management and development of tropical secondary forest in Latin America: Pucallpa, Peru, 2-6 June 1997. (Memorias del Taller Internacional sobre el estado actual y potencial de manejo y desarrollo del bosque secundario tropical en América Latina: Pucallpa, Perú, 2-6 junio 1997). Venezuela, Secretaría Pro Tempore, 106–120 pp. (In Spanish).

Finegan, B., Sabogal, C. 1988. The development of sustainable production systems in lowland humid tropical forests: a case study in Costa Rica. (El desarrollo de sistemas de producción sostenible en bosques tropicales húmedos de bajura: un estudio de caso en Costa Rica). – El Chasqui, 17, 1–22. (In Spanish).

Forero-Peña, L.A, Leiva Rojas, E.I., Ramírez Pisco, R. 2020. Characterization of the intervened secondary forest in Bajo Calima, Buenaventura. (Caracterización del bosque secundario intervenido en el Bajo Calima, Buenaventura). – Albarán Castro, N.J., Forero-Peña, L.A., Fernández-Méndez, F. (eds.). Avances y Perspectivas de Investigación en Biodiversidad y su Uso en el Territorio Colectivo del Bajo Calima. Ibagué, Colombia, Universidad del Tolima, 47–57. (In Spanish).

Forero-Peña, L.A., Mora-Delgado, J. 2017. Livelihoods and family gardens in the black community of the lower basin of the Calima river, Colombia. (Medios de vida y huertos familiares en la comunidad negra de la cuenca baja del río Calima, Colombia). – Agroforestería Neotropical, 7, 63–71. (In Spanish).

Forero-Peña, L.A., Ordóñez, H.R. 1992. Structural ecological study of the second growth forest (5 to 20 years old) in Bajo Calima. Buenaventura, Colombia. (Estudio ecológico estructural del bosque de segundo crecimiento (5 a 20 años de edad) en el Bajo Calima. Buenaventura, Colombia). – degree work. Ibagué, Colombia, Universidad del Tolima, Facultad de Ingeniería Forestal. 105 pp. (In Spanish).

Guariguata, M.R., Ostertag, R. 2002. Secondary succession. (Sucesión secundaria). – Guariguata, M.R., Kattan, G.H. (eds.). Ecology and conservation of Neotropical forests. (Ecología y conservación de bosques neotropicales). Cartago, Costa Rica, Editorial Tecnológica, 592–623. (In Spanish).

Hayward, R.M., Banin, L.F., Burslem, D.F.R.P., Chapman, D.S., Philipson, C.D., Cutler, M.E.J., Reynolds, G., Nilus, R., Dent, D.H. 2021. Three decades of post-logging tree community recovery in naturally regenerating and actively restored dipterocarp forest in Borneo. – Forest Ecology and Management, 488, 119036. http//doi.org/10.1016/j.foreco.2021.119036.

Hüller, A., Rauber, A., Wolski, M.S., Almeida, N.L., Wolski, S.R.S. 2011. Natural regeneration of tree and shrub component in Santo Ângelo Natural Municipal Park, RS. (Regeneração natural do componente arbóreo e arbustivo do Parque Natural Municipal de Santo Ângelo-RS). – Revista SBAU, 6(1), 25–35. http://dx.doi.org/10.5380/revsbau.v6i1.66387. (In Portuguese).

IDEAM (Instituto De Hidrología, Meteorología y Estudios Ambientales). 2008. The proportion of land covered with forests with respect to the continental area of the country. (Proporción de la superficie de tierras cubiertas con bosque con respecto a la superficie continental del país). Subdirección de Ecosistemas e Información ambiental. Grupo Bosques Reporte al Sistema de Información del Medio Ambiente – SIMA- de la Comunidad Andina de Naciones- CAN. Bogotá, Colombia, 6 pp. (In Spanish).

Ladrach, W.E., Mazuera, H.G. 1985. Sources and characteristics of the natural regeneration in a humid tropical rain forest after clear-cutting. – Ladrach, W.E. (ed.). Forest Research in the Bajo Calima Concession. Ninth Annual Report. Cali, Colombia, Cartón de Colombia S.A. 228 pp.

Louman, B., Quirós, D., Nilsson, M. 2001. Silviculture of humid broadleaf forests with emphasis on Central America. (Silvicultura de Bosques Latifoliados Húmedos con Énfasis en América Central). Turrialba, Costa Rica, CATIE (Centro Agronómico Tropical de Investigación y Enseñanza). 265 pp. (In Spanish).

Martínez, H. 2006. Silvicultural ecological analysis, for management purposes, of the secondary forest of the village of Las Brisas, Buenaventura, Valle del Cauca, Colombia. (Análisis ecológico silvicultural, con fines de manejo, del bosque secundario de la vereda las Brisas, Buenaventura, Valle del Cauca, Colombia). – Doctoral thesis. Cali, Colombia, Universidad del Valle. 90 pp. (In Spanish).

Mazuera, G.H. 1985. Composition and growth of four to fifteen-year-old natural regeneration in the Bajo Calima Concession. – Ladrach, W.E. (ed.). Forest Research in the Bajo Calima Concession. Ninth Annual Report. Cali, Colombia, Cartón de Colombia S.A., 145–170.

Melo, C.L.S.M.S., Ferreira, R.L.C., Silva, J.A.A., Machuca, M.Á.H., Cespedes, G.H.G. 2019. Dynamics of dry tropical forest after three decades of vegetation suppression. – Floresta e Ambiente, 26(3), e20171163. https://doi.org/10.1590/2179-8087.116317.

Ngo Bieng, M.A., Finegan, B., Sist, P. 2022. Active restoration of secondary and degraded forests in the context of the UN Decade on Ecosystem Restoration. – Forest Ecology and Management, 503, 119770. https://doi.org/10.1016/j.foreco.2021.119770.

Ngo Bieng, M.A., Oliveira, M.S., Roda, J.-M., Boissière, M., Hérault, B., Guizol, P., Villalobos, R., Sist, P. 2021. Relevance of secondary tropical forest for landscape restoration. – Forest Ecology and Management, 493, 119265. https://doi.org/10.1016/j.foreco.2021.119265.

Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., van Breugel, M., Lebrija-Trejos, E., Meave, J.A., Vandermeer, J., Williamson, G.B., Finegan, B., Mesquita, R., Chazdon, R.L. 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. – Proceedings of the National Academy of Sciences, 112(26), 8013–8018. https://doi.org/10.1073/pnas.1500403112.

Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.-H., Vílchez-Alvarado, B. 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. – Ecology Letters, 12(5), 385–394. https://doi.org/10.1111/j.1461-0248.2009.01292.x.

Osazuwa-Peters, O.L., Chapman, C.A., Zanne, A.E. 2015. Selective logging: does the imprint remain on tree structure and composition after 45 years? – Conservation Physiology, 3(1), cov012. https://doi.org/10.1093/conphys/cov012.

Pacheco-Pascagaza, A.M. 2020. Degradation of the Bajo Calima forests: structural variations of the forest derived from synthetic aperture radar images. (Degradación de los bosques del Bajo Calima: variaciones estructurales del bosque derivadas de imágenes de radar de apertura sintética). – Albarán Castro, N.J., Forero-Peña, L.A., Fernández-Méndez, F. (eds.). Avances y Perspectivas de Investigación en Biodiversidad y su Uso en el Territorio Colectivo del Bajo Calima. Ibagué, Colombia, Universidad del Tolima, 169–183. (In Spanish).

Peña-Claros, M. 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. – Biotropica, 35(4), 450–461. https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1744-7429.2003.tb00602.x.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Boukili V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., de Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., de Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A. 2016. Biomass resilience of Neotropical secondary forests. – Nature, 530, 211–214. https://doi.org/10.1038/nature16512.

Poorter, L., Craven, D., Jakovac, C.C., van der Sande, M.T., Amissah, L., Bongers, F., Chazdon, R.L., Farrior, C.E., Kambach, S., Meave, J.A., Muñoz, R., Norden, N., Rüger, N., van Breugel, M., Almeyda Zambrano, A.M., Amani, B., Andrade, J.L., Brancalion, P.H.S., Broadbent, E.N., de Foresta, H., Dent, D.H., Derroire, G., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Fantini, A.C., Finegan, B., Hernández-Jaramillo, A., Hernández-Stefanoni, J.L., Hietz, P., Junqueira, A.B., N'dja, J.K., Letcher, S.G., Lohbeck, M., López-Camacho, R., Martínez-Ramos, M., Melo, F.P.L., Mora, F., Müller, S.C., N'Guessan, A.E., Oberleitner, F., Ortiz-Malavassi, E., Pérez-García, E.A., Pinho, B.X., Piotto, D., Powers, J.S., Rodríguez-Buriticá, S., Rozendaal, D.M.A., Ruíz, J., Tabarelli, M., Teixeira, H.M., Valadares de Sá Barretto Sampaio, E., van der Wal, H., Villa, P.M., Fernandes, G.W., Santos, B.A., Aguilar-Cano, J., de Almeida-Cortez, J.S., Alvarez-Davila, E., Arreola-Villa, F., Balvanera, P., Becknell, J.M., Cabral, G.A.L., Castellanos-Castro, C., de Jong, B.H.J., Nieto, J.E., Espírito-Santo, M.M., Fandino, M.C., García, H., García-Villalobos, D., Hall, J.S., Idárraga, A., Jiménez-Montoya, J., Kennard, D., Marín-Spiotta, E., Mesquita, R., Nunes, Y.R.F., Ochoa-Gaona, S., Peña-Claros, M., Pérez-Cárdenas, N., Rodríguez-Velázquez, J., Villanueva, L.S., Schwartz, N.B., Steininger, M.K., Veloso, M.D.M., Vester, H.F.M., Vieira, I.C.G., Williamson, G.B., Zanini, K., Hérault, B., 2021. Multidimensional tropical forest recovery. – Science, 374(6573), 1370–1376. https://doi.org/10.1126/science.abh3629.

Quinto Mosquera, H., Moreno Hurtado, F. 2011. Dynamics of tree aboveground biomass in a tropical rain forest of the Chocó Biogeográfico. (Dinámica de la biomasa aérea en un bosque pluvial tropical del Chocó Biogeográfico). – Revista Facultad Nacional de Agronomía, 64(1), 5917–5936. (In Spanish).

Rodríguez, J.C. 1989. Considerations on the Biomass, Chemical Composition and Dynamics of the Tropical Rainforest of Colinas Bajas. Bajo Calima. Buenaventura, Colombia. (Consideraciones sobre la Biomasa, Composición Química y Dinámica del Bosque Pluvial Tropical de Colinas Bajas. Bajo Calima. Buenaventura, Colombia). Serie documentación No.16. Bogotá, Colombia, Corporación Nacional de Investigación y Fomento Forestal (CONIF). 36 pp. (In Spanish with English summary).

Saldarriaga, J.G., West, D.C., Tharp, M.L., Uhl, C. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. – Journal of Ecology, 76(4), 938–958.

Uhl, C., Jordan, C.F. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. – Ecology, 65(5), 1476–1490. https://doi.org/10.2307/1939128.

Valencia, R., Foster, R.B., Villa, G., Condit, R., Svenning, J.-C., Hernández, C., Romoleroux, K., Losos, E., Magård, E., Balslev H. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. – Journal of Ecology, 92(2), 214–229. https://doi.org/10.1111/j.0022-0477.2004.00876.x.

Vallejos, O. 1996. Productivity and relationships of the site index with physiographic, edaphoclimatic and foliar variables for *Tectona grandis* L.f. *Bombacopsis quinatum* (Jacq.) Dugand and *Gmelina arborea* Roxb. in Costa Rica. (Productividad y relaciones del índice de sitio con variables fisiográficas, edafoclimáticas y foliares para *Tectona grandis* L.f. *Bombacopsis quinatum* (Jacq.) Dugand y *Gmelina arborea* Roxb. en Costa Rica). – Master thesis. Turrialba, Costa Rica, CATIE. 147 pp. (In Spanish).

Wright, J.A. 1997. Forest management and research in the Bajo Calima Concession, Colombia. (Manejo e investigación forestal en la Concesión del Bajo Calima, Colombia). – Sabogal, C., Camacho, M., Guariguata, M.R. (eds.). Practical experiences and research priorities and silviculture of natural forests in Tropical America. (Experiencias prácticas y prioridades de investigación y silvicultura de bosques naturales en América Tropical). – Proceedings of the Seminar-Workshop, Pucallpa, Peru, 17-21 June 1996. Turrialba, Costa Rica, CATIE, 137–142. (In Spanish).

Yan, J., Wang, Y., Zhou, G., Zhang, D. 2006. Estimates of soil respiration and net primary production of three forests at different succession stages in South China. – Global Change Biology, 12(5), 810–821.

Zambiazi, D.C., Fantini, A.C., Piotto, D., Siminski, A., Vibrans, A.C., Oller, D.C., Piazza, G.E., Peña-Claros, M. 2021. Timber stock recovery in a chronosequence of secondary forests in Southern Brazil: adding value to restored landscapes. – Forest Ecology and Management, 495, 119352. https://doi.org/10.1016/j.foreco.2021.119352.

Zent, S. 1995. Classification, exploitation, and composition of secondary forests in the Upper Cuao River, Amazonas State, Venezuela. (Clasificación, explotación y composición de bosques secundarios en el Alto Río Cuao, Estado Amazonas, Venezuela). – Scientia Guaianae, 5, 79–113. (In Spanish).

Received March 05, 2022, revised November 11, 2022, accepted November 15, 2022