(1), 10.0 – 14.9 cm (2), 15.0 – 19.9 cm (3), 20.0 – 24.9 cm (4), 25.0 – 29.9 cm (5), and ≥ 30.0 cm (6). For comparisons, this distribution was done twice: in 1998 and 2010 (one year and 12 years after logging).

The diameter growth was calculated by the difference between diameters measured only in the alive trees along all five monitoring periods (1998-1999, 1998-2000, 1998-2001, 1998-2007, and 1998-2010), according to the formula $(DBH_{final} - DBH_{initial})/T_{(time)}$. From this measure, the Periodic Annual Increment in diameter (PAIdbh) was calculated.

The analysis of variance (ANOVA) was done through a Generalized Linear Model (GLM) for gap's size (small, medium, and large), distance in relation to the gap's border (plots far away 10, 20, 30, 40, and 50 m from the gap's border), and the time of experiment monitoring (12 years) on the dependent variable (PAIdbh). The data were analyzed through repeated measures ANOVA and, in case of significant differences among treatments, the post-hoc Tukey test was applied to compare means. All statistical analyses were run with the software R version 3.6.1 (R Development Core Team, 2019), at $p < 0.05$ of significance.

Results

Seedling density and diameter distribution of *Theobroma subincanum*

Seedling density in relation to the distance of the gap's border decreased up to 30 m from the gap's border, regardless the year after logging. The number of individuals per plot reduced from 7.00 at 10 m to 3.00 at 30 m from the gap's border. Density increased again at 40 m and 50 m after logging (Fig. 2).

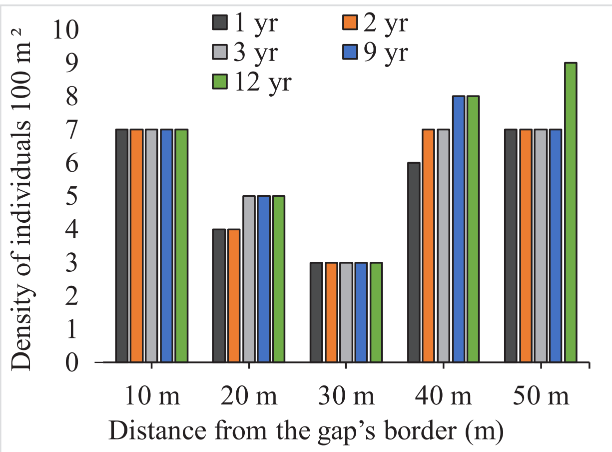

Figure 2. Seedling density of seedlings ≥ 5 cm in DBH of the species *Theobroma subincanum* in relation to seedlings' distances from the gap's border towards the forest in a managed forest after RIL in the Experimental Field of Moju, Eastern Amazon, Brazil.

In the first measurement after RIL (1998), the seedling density of *Theobroma subincanum* with DBH ≥ 5 cm, regardless the treatment, was 15.00 seedlings ha^{-1} and in the last, 12 years after RIL (2010), was 17.78 seedlings ha^{-1} (Fig. 3). Although varying among diameter classes, the diameter distribution of *T. subincanum* maintained an increasing shape in the two first classes (5.0-9.9 and 10.0-14.9) and a decreasing shape in the third class forwards (15.0 cm) during the entire monitoring period (Fig. 3). The largest changes in the distribution of individuals were observed in the first class (decrease) and in the third and fourth class (increase).

PAIdbh in relation to distance from logging gap's border and time after RIL

There was a significant difference in the Periodic Annual Increment in diameter (PAIdbh) of *T. subincanum* in relation to the distance of the individual to the gap's border ($p = 0.001$). The shorter is distance of the individual from the gap's border the higher is its PAIdbh (Fig. 4). There was a significant difference in the two first years after RIL among all plot distances in relation to the gap's border (10, 20, 30, 40, and 50 m). The 10 m distance presented higher increment (0.75 cm year^{-1}, $F_{4,63} = 4.97$, $p = 0.002$) in the two first years. The year following RIL also influenced positively the seedlings growth ($p = 0.001$). PAIdbh was significantly higher in the first year after the application of RIL and decreased significantly from the second year after logging. From nine years after logging onwards, growth stagnated where no more differences in PAIdbh were observed in both plots distance from the gaps' border and time ($p = 0.161$). At the end of 12 years of monitoring, the seedlings had an average increase of 1.82 cm in diameter, which represented an average PAIdbh of 0.15 cm year^{-1}.

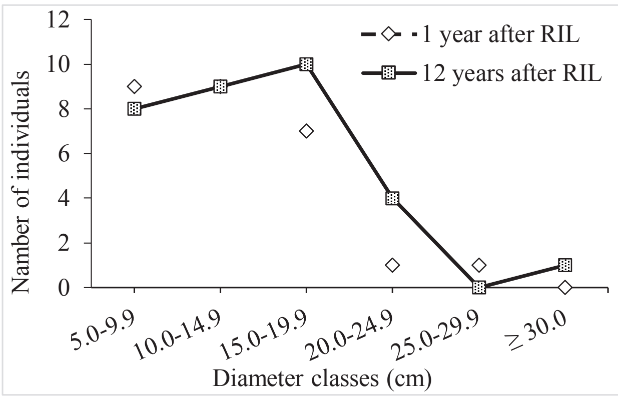

Figure 3. Diameter distribution of *Theobroma subincanum* from DBH ≥ 5 cm and intervals of DBH = 5 cm one year and 12 years after reduced impact logging (RIL) in a managed forest after RIL in the Experimental Field of Moju, Eastern Amazon, Brazil.

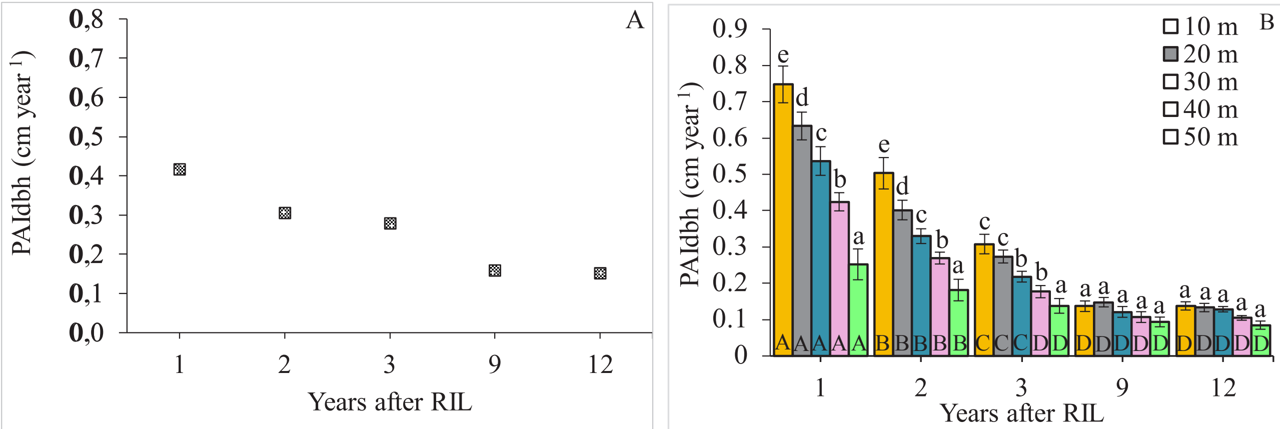

Figure 4. Mean of the Periodic Annual Increment in diameter (PAIdbh) of *Theobroma subincanum* along 12 years of monitoring following reduced impact logging (RIL) (A) and plots distances in relation to the gaps' border (B) in a managed forest after RIL in the Experimental Field of Moju, Eastern Amazon, Brazil. Means followed by the same letter do not differ statistically each other, lower cases indicate differences among distances in the same year while upper cases indicate indicate differences in time in the same distance (ANOVA followed by the post-hoc Tukey test, p < 5%).

PAIdbh in relation to gap size and plots direction in cardinal points

In relation to gap size, seedlings placed around small, medium, and large logging gaps did not present significant differences in PAIdbh (p= 0.308). Growth was higher during the three first years for all gap sizes (Fig. 5a). Seedlings around medium size gaps had higher PAIdbh in the two first years, however this was not statistically significant. Regarding cardinal points, there was no significant differences in PAIdbh (p= 0.503) in relation to each direction. Growth was highest in the first year after logging in all cardinal directions and started decreasing in response to canopy closing (Fig. 5b).

Discussion

Seedling density and diameter distribution of Theobroma subincanum

Seedling density of *Theobroma subincanum* had no relation with distances from the gap's border. The density of individuals reduced in the first 30 m and, from the distance of 40 m it increased again. This result shows that the distance from the gap's border had influence on *T. subincanum* growth (Fig. 4), but not on its density (Fig. 2).

The density of individuals of *T. subincanum* did not have any significant change during 12 years of monitoring (Fig. 3). A stable density indicates that recruitment

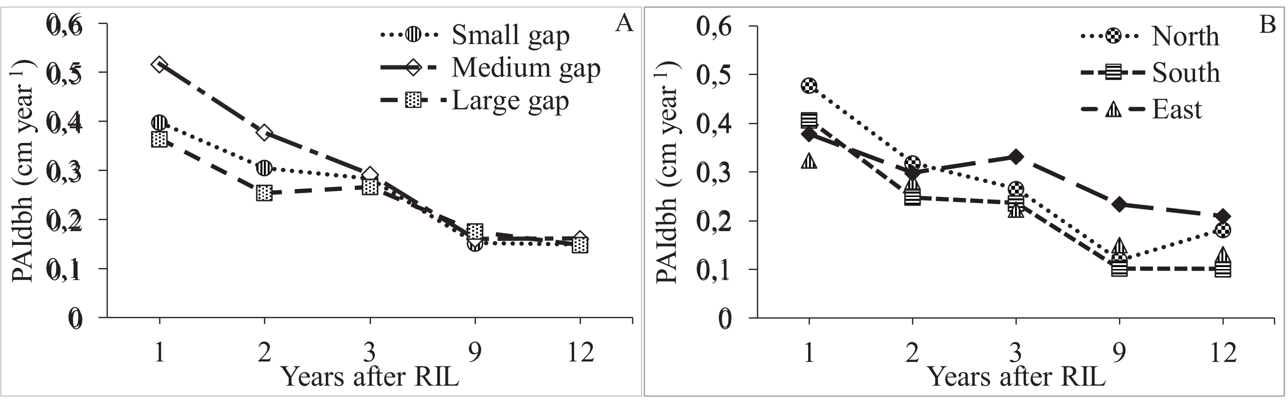

Figure 5. (a) Periodic Annual Increment in diameter (PAIdbh) in relation to gap size (small, medium, and large) and (b) Periodic Annual Increment in diameter (PAIdbh) in relation to cardinal points (North, South, East, West of the species *Theobroma subincanum* in a managed forest after reduced impact logging (RIL) in the Experimental Field of Moju, Eastern Amazon, Brazil. Differences among gap size and cardinal points are not significant (p>0.05) for all years after treatment.

and mortality rate were constant over time. Hence, the influence of logging gaps on *T. subincanum* was restricted to trees' growth and not to population dynamics, at least when considered individuals ≥ 5 cm in DBH. This is an indication that the species takes indirect advantage of canopy gaps caused by the fall of harvested trees.

The diameter distribution of *T. subincanum* in different periods showed the presence of seedlings in all classes, one and 12 years after logging, with no steep alteration along time. One year after logging, the number of individuals in the two first diameter classes (5.0-9.9 and 10.0-14.9) remained stable, distributed in a decreasing pattern from the third class forwards (15.0-19.9). Twelve years after logging, the number of individuals in class 5.0-9.9 diminished as a consequence of mortality and switch of individuals to upper diameter classes (Fig. 3). This distribution pattern is proper of shade-tolerant species. Although shade-tolerant species grow in conditions of close canopy and understory, they benefit from direct or indirect sunlight coming from canopy gaps, as well as direct light flecks that cross canopy and attain the soil (Jardim, 2015). Individuals of *T. subincanum* were distributed according to a reverse "J" shape, the most common distribution pattern of native tropical forests. This curve indicates a population dynamic balance of a shade-tolerant species, where most of the individuals are concentrated in smaller diameter classes.

PAIdbh in relation to distance from logging gap's border and time after RIL

In all analyzed plots, *T. subincanum* obtained higher growth in the first year of monitoring, which is related to higher availability of sun radiation reaching the forest floor. However, the longer is the plot distance from the border the lower is PAIdbh. According to Jardim (2015), shade-tolerant species benefit from the solar radiation coming from logging gaps, as well as small flecks of direct solar radiation coming from logging gaps or forest canopy. In studies carried out in the Tapajós National Forest, Eastern Amazon, Schwartz *et al*. (2012) observed that individuals of shade-tolerant species under total illumination obtained better growth rates than those under partial or with no illumination. Shade-tolerant species are sensible to low quantities of light, as even those plots far 40 and 50 m away from the gaps' border, two years after RIL, still presented statistical differences from each other. The difference in growth between the 40 and 50 m plots only disappeared in the third year after RIL (Fig. 4).

Theobroma subincanum stabilized its growth in diameter nine years after logging. According to Dionisio *et al.* (2017, 2018) growth, mortality, and recruitment rates in managed forests under RIL in the Eastern Amazon stabilize between seven and eleven years after logging.

PAIdbh in relation to gap size and plots direction in cardinal points

The lack of difference in PAIdbh of *T. subincanum* when compared to gap size shows that small gaps, even when opened by branches fall, are sufficient to speed up growth of shade-tolerant species. Although the literature shows influence of gap size on species richness and growth, *T. subincanum* did not respond to this variable. This can be a pattern of responses of shade-tolerant species to light (Schwartz *et al*., 2012). While pioneer species demand high amounts of light to grow, shade-tolerant species need minimum amounts of light to develop. Any small increase in light is enough to trigger positive growth responses from shade-tolerant species. Large gaps promote higher germination and growth of individuals belonging to pioneer and light-demanding species and promote growth of shade-tolerant species. On the other hand, small and medium size gaps have low influence on germination and growth of pioneer and light-demanding species, but still promote growth of shade-tolerant species (Brokaw, 1985; Kobe *et al*., 1995).

Like gap size, the plots direction following cardinal points also did not interfere on *T. subincanum* growth. The dissimilar light availability in different cardinal points around the logging gap due to sunlight movements was not sufficient to promote different responses in growth of *T. subincanum*. Light incidence had great effect on *T. subincanum* growth, but not in relation to cardinal points around the gap. The location of a given individual inside a canopy gap can reflect on its growth, where there are differences in sunlight incidence in function of daytime (Denslow, 1980; Barton, 1984; Jardim, 2015), but not inside the forest immediately around the gap. Despite the fact that individuals of *T. subincanum* grew better in a light gradient, they did not respond to their location in cardinal points.

Conclusions

There were no changes in density and population structure of the shade-tolerant species *Theobroma subincanum* distributed in different distances around different size logging gaps created by reduced impact logging (RIL). The species presented diameter distribution in reverse "J" shape, which remained unchanged along 12 years of monitoring after RIL, only with individuals moving to higher diameter classes by growing. There was higher growth, measured in Periodic Annual Increment in diameter (PAIdbh), of *T. subincanum* up to three years after RIL, and a further stabilization nine years after logging.

Individuals of *T. subincanum* responded to the higher entrance of indirect sunlight caused by the canopy gap, they presented a growing gradient inversely proportional to the distance from the gap's border. No differences in growing responses were observed in individuals of *T. subincanum* in relation to gap size and the plots direction in cardinal points around the canopy gap.

Acknowledgements

We are grateful to Embrapa Eastern Amazon to provide study area and facilities to carry on our experiment in the Experimental Field of Moju.

References

Abiyu A, Mokria M, Gebrekirstos A, Bräuning A, 2018. Tree-ring record in Ethiopian church forests reveals successive generation differences in growth rates and disturbance events. For Ecol Manage, 409: 835-844. https://doi.org/10.1016/j.foreco.2017.12.015

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G, 2013. Köppen's climate classification map for Brazil. Meteorol Z, 22 (6): 711-728. https://doi.org/10.1127/0941-2948/2013/0507

Alverson WS, Whitlock BA, Nyffeler R, Bayer C, Baum DA, 1999. Phylogeny of the core Malvales: evidence from ndhF sequence data. Am J Bot, 86 (10): 1474-1486. https://doi.org/10.2307/2656928

Barton AM, 1984. Neotropical pioneer and shade - tolerant tree species: do they partition tree fall gaps? Trop Ecol 25: 196-202.

Brokaw NVL, 1985. Gap-phase regeneration in a tropical forest. Ecololgy 66 (3): 682-687. https://doi.org/10.2307/1940529

Dardengo JFE, Rossi AAB, Silva BM, Silva IV, Silva CJ, Sebbenn AM, 2016. Diversity and spatial genetic structure of a natural population of Theobroma speciosum (Malvaceae) in the Brazilian Amazon. Internat J Trop Biol, 64 (3): 1091-1100. https://doi.org/10.15517/rbt.v64i3.21461

Darrigo MR, Venticinque EM, Santos FAM, 2016. Effects of reduced impact logging on the forest regeneration in the central Amazonia. Forest Ecol Manage, 360: 52-59. https://doi.org/10.1016/j.foreco.2015.10.012

Denslow JS, 1980. Gap partitioning among tropical rain forest trees. Biotropica, 12: 47-55. https://doi.org/10.2307/2388156

Dionisio LFS, Schwartz G, Lopes JC, Oliveira FA, 2018. Growth, mortality, and recruitment of tree species in an Amazonian rainforest over 13 years of reduced impact logging. Forest Ecol Manage, 430: 150-156. https://doi.org/10.1016/j.foreco.2018.08.024

Dionisio LFS, Schwartz G, Lopes JC, Santos GGA, Oliveira FA, 2017. Mortality of stocking commercial trees after reduced impact logging in eastern Amazonia. Forest Ecol Manage, 401: 1-7. https://doi.org/10.1016/j.foreco.2017.06.060

Grogan JS, Jennings SB, Landis RM, Schulze A, Baima AMV, Lopes JCA, Norghauer JM, Oliveira LR, Pantoja F, Pinto D, Silva JNM, Vidal E, Zimmerman BL, 2008. What loggers leave behind: impacts on big-leaf mahogany (Swietenia macrophylla) commercial populations and potential for post-logging recovery in the Brazilian Amazon. Forest Ecol Manage, 255: 269-281. https://doi.org/10.1016/j.foreco.2007.09.048

Instituto Brasileiro de Geografa e Estatística - IBGE, 2012. Manual técnico da vegetação brasileira. 2. ed. Rio de Janeiro. 275 pp.

Jardim FCS, 2015. Natural regeneration in tropical forests. Rev Ci Agr, 58 (1): 105-113. https://doi.org/10.4322/rca.1676

Kobe RK, Pacala SW, Silander JRJA, Canham CD, 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol Appl 5 (2): 517-532. https://doi.org/10.2307/1942040

Neves RLP, Schwartz G, Lopes JCA, Leão FM, 2019. Post-harvesting silvicultural treatments in canopy logging gaps: medium-term responses of commercial tree species under tending and enrichment planting. Forest Ecol Manage, 451: Article 117521. https://doi.org/10.1016/j.foreco.2019.117521

R core team. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Version 3.6.1. [Vienna]: R Core Team, 2019.

Rivas LH, Giustina LD, Luz LN, Karsburg IV, Pereira TNS, Rossi AAB, 2013. Genetic diversity in natural populations of Theobroma subincanum Mart. in the Brazilian Amazon. Genet Mol Res, 12 (4): 4998-5006. https://doi.org/10.4238/2013.October.24.12

Schwartz G, Falkowski V, Peña-Claros M, 2017. Natural regeneration of tree species in the Eastern Amazon: short-term responses after reduced-impact logging. Forest Ecol Manage, 385: 97-103. https://doi.org/10.1016/j.foreco.2016.11.036

Schwartz G, Lopes JCA, Kanashiro M, Mohren GMJ, Peña-Claros M, 2014. Disturbance level determines the regeneration of commercial tree species in the Eastern Amazon. Biotropica, 46 (2): 148-156. https://doi.org/10.1111/btp.12096

Schwartz G, Lopes JCA, Lopes JCA, Mohren GMJ, Peña-Claros M, Kanashiro M, 2012. Mid-term effects of reduced-impact logging on the regeneration of seven tree commercial species in the Eastern Amazon. Forest Ecol Manage, 274: 116-125. https://doi.org/10.1016/j.foreco.2012.02.028

Silva BM, Rossi AAB, Dardengo JFE, Silva CR, Silva IV, Silva ML, Silva CJ, 2015. Genetic structure of natural populations of Theobroma in the Juruena National Park, Mato Grosso State, Brazil. Genet Mol Res, 14 (3): 10365-10375. https://doi.org/10.4238/2015.September.1.3

Whitlock MC, Ingvarsson PK, Hatfield T, 2000. Local drift load and the heterosis of interconnected populations. Hered, 84 (4): 452-457. https://doi.org/10.1046/j.1365-2540.2000.00693.x

Whitmore TC, 1989. Canopy gaps and the two major groups of forest trees. Ecology 70: 536-538. https://doi.org/10.2307/1940195

Yguel B, Piponiot C, Mirabel A, Dourdain A, Hérault B, Gourlet-Fleury S, Forget PM, Fontaine C, 2019. Beyond species richness and biomass: impact of selective logging and silvicultural treatments on the functional composition of a neotropical forest. Forest Ecol Manage, 433: 528-534. https://doi.org/10.1016/j.foreco.2018.11.022