Effects of liana load, tree diameter and distances between conspecifics on seed production in tropical timber trees

Jacob Nabe-Nielsen [a,b,*], Johannes Kollmann [c], Marielos Peña-Claros [d,e]

[a] Section for Climate Effects and System Modelling, National Environmental Research Institute, University of Aarhus, Roskilde, Denmark
[b] Centre for Integrated Population Ecology,[1] Denmark
[c] Department of Agriculture and Ecology, Copenhagen University, Copenhagen, Denmark
[d] Instituto Boliviano de Investigación Forestal, P.O. Box 6204, Santa Cruz, Bolivia
[e] Forest Ecology and Forest Management Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

ABSTRACT

Seed production in tropical timber trees is limited by abiotic resources, pollination and pre-dispersal seed predation. Resource availability is influenced by the number of competing trees and by lianas that often reach high densities in disturbed parts of tropical forests. The distance between conspecific trees affects pollination efficiency and seed predation intensity, and may therefore indirectly affect the long-term sustainability of selective logging. Here we investigate how reproductive status and the number of seeds dispersed per tree are affected by liana load, distance to the nearest conspecifics, number of competing neighbours and tree diameter in the timber trees Cariniana ianeirensis and Terminalia oblonga. The study is based on a large-scale silvicultural experiment in lowland Bolivia. We found that the reproductive status of the two species was negatively correlated with liana cover and positively with tree diameter. In C. ianeirensis the most liana-infested trees dispersed fewer seeds. In T. oblonga the intensity of pre-dispersal seed predation decreased with distance to the nearest conspecifics. There was no evidence that seed viability or seed production decreased with distance to nearest conspecifics in either species as would be expected if isolation resulted in increased self-pollination. Our results indicate that reproduction can be severely reduced in timber trees if the largest, most healthy and least liana-covered trees are logged, but that liana cutting on the remaining seed trees can considerably improve seed production. In some species seed production may be further improved by ensuring that seed trees are located far apart.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

The regeneration of tropical trees is often limited both by the availability of seeds and of microsites where seedlings can successfully establish (Eriksson and Ehrlen, 1992; Dalling et al., 2002; De Steven and Wright, 2002). Selective logging is therefore likely to have a large impact on regeneration by reducing the density of seed-dispersing trees and thus seed production (Ghazoul et al., 1998; Ghazoul and McLeish, 2001). As forestry can only be sustainable when timber extraction is balanced by recruitment, it is important to understand how seed production can be maintained or enhanced through improved forest management.

One of the characteristic features of tropical forests is the prevalence of lianas that often attain high densities in disturbed areas (Putz, 1984; Laurance et al., 2001). Lianas compete with trees for resources, thereby suppressing tree growth (Clark and Clark, 1990; Gerwing, 2001; Grauel and Putz, 2004; Campanello et al., 2007) and reducing reproduction (Wright et al., 2005). In addition, stand density negatively affects tree growth and fecundity (Guariguata, 1999), whereas seed production is positively correlated with tree diameter (Snook et al., 2005). A better understanding of the relative impact of liana densities, stand density and tree diameter on seed production would be of great value for improving the management of selectively logged tropical forests.

The larger distances between neighbouring trees in selectively logged forests can also have a negative impact on reproduction by resulting in decreased levels of cross-pollination (Hall et al., 1996; Ghazoul and McLeish, 2001). This may result in lower seed production or poorer seed viability in individuals that are far from the nearest conspecifics. Alternatively the increased distances between the remaining trees may result in reduced

* Corresponding author at: National Environmental Research Institute, University of Aarhus, Frederiksborgvej 399, P.O. Box 358, DK-4000 Roskilde, Denmark. Tel.: +45 46301944; fax: +45 46301914.
E-mail address: nabe@dmu.dk (J. Nabe-Nielsen).
[1] www.cipe.dk.

density-dependent seed and seedling predation (Augspurger, 1983; Clark and Clark, 1984; Cintra, 1997), which may partially offset the negative effects that logging has on seed production.

The aims of the current study were to investigate whether variations in liana load, distance between conspecific trees, stand density and tree diameter were associated with (1) reproductive status of individual trees, (2) variation in seed germination and predation (3), and production of viable seeds on reproductive trees. Finally, (4) we compared total number of viable seeds in logged and unlogged areas in order to assess if logging had other effects on reproduction that were not captured in the previous analyses. We selected the two timber species *Cariniana ianeirensis* and *Terminalia oblonga* for the study. Both species are common and economically important in the tropical forests of lowland Bolivia.

2. Methods

2.1. Study area

The study was conducted in a semi-deciduous tropical moist forest in lowland Bolivia within the 100,000 ha forestry concession of Agroindustria Forestal La Chonta (15°45′S, 62°60′W) during July–November 2002. Mean annual temperature in the area is 24.5 °C and annual rainfall is 1580 mm, with 5 months receiving <100 mm (May–September). During the dry season the area is affected by strong winds from the south and by occasional wildfires (Blate, 2005).

The forest has a canopy height of ∼25 m. It is characterized by abundant treefall gaps and numerous emergent trees (e.g. *Ficus boliviana* C.C. Berg that reached a height of 50 m; J. Nabe-Nielsen, unpubl. data). For trees >10 cm dbh (diameter at breast height, measured 1.3 m above ground), the forest has an average density of 367 stems ha^{-1}, a basal area of 19.3 m^2 ha^{-1}, and 59 tree species ha^{-1}. Large areas are covered by lianas (predominately species of *Clitostoma*, *Pleonotoma*, *Serjania* and *Hippocratea*; Alvira et al., 2004), and pioneer species (e.g. *Triplaris americana* L. and *Urera baccifera* L.) are abundant, both in selectively logged and in unlogged parts of the forest. There are 160 tree species identified at La Chonta, 24 of which are considered to be merchantable for timber. The site has been used for numerous studies (e.g. Fredericksen et al., 2001; Fredericksen and Pariona, 2002; Alvira et al., 2004; Schiøtz et al., 2006; Nabe-Nielsen et al., 2007; Peña-Claros et al., 2008). It contains a unique logging experiment conducted by Instituto Boliviano de Investigación Forestal (IBIF), the Long-term Silvicultural Research Program (LTSRP). The present study was conducted in four of the twelve 450-m × 600-m LTSRP plots established in La Chonta (27 ha per plot, 108 ha in total). The plots were located 0.5–2.5 km apart. Two of them had been used for selective logging following the current Bolivian prescriptions 1 year prior to the study (the 'Normal' treatment in Peña-Claros et al., 2008), and two had been left as unlogged reference plots surrounded by 150 m buffer zones. Lianas growing on commercial trees had been cut at least 6 months before logging.

2.2. Study species

Seed production and seed viability were studied in the timber tree species *Cariniana ianeirensis* R. Knuth (Lecythidaceae) and *Terminalia oblonga* Steud. (Combretaceae) (henceforth referred to by genus names only). Both species regenerate poorly in the study area (Pariona et al., 2003; Schiøtz et al., 2006) and very little is known about the mechanism behind their poor regeneration (Mostacedo and Fredericksen, 1999). Both species are monoecious and bee-pollinated (Prance and Mori, 1979; Mori and Boeke, 1987; Gentry, 1993). They rarely or never become reproductive before

reaching 20 cm dbh (J. Nabe-Nielsen, unpubl. data). The seeds of *Terminalia* are small and winged, but poorly dispersed (rarely >35 m; J. Nabe-Nielsen, unpubl. data), whereas *Cariniana* produces large winged seeds that may disperse >35 m from tall parent trees in windy weather. In La Chonta the seeds of *Cariniana* were frequently predated before dispersal by macaws that were able to open the woody capsules (J. Nabe-Nielsen, unpubl. data).

2.3. Assessing the reproductive status of individual trees

The reproductive status of the study trees, i.e. whether they produced seeds or not, was recorded for all individuals >20 cm dbh in the four plots. Liana load (estimated as percent crown cover), distance to conspecifics, number of competing neighbours (trees of all species >20 cm dbh, <10 m away) and tree dbh were recorded for all individuals. Instead of using distance to conspecifics directly we used a nearest neighbour index (NNI), which was calculated as the geometric mean of the distances to the two nearest conspecifics, i.e. as the square root of the product of the first and second nearest neighbour distances (cf. Ghazoul and McLeish, 2001). This allowed us to combine two distances into a single measure that has proved to be valuable in other studies.

To evaluate how liana load, distance to conspecifics, number of competing neighbours and dbh affected the reproductive status of the trees, we employed a logistic regression for each of the two study species. This yielded estimates of variations in the probability that trees produced seeds. All explanatory variables were Log$_e$-transformed. Due to the risk of spatial autocorrelation, the significance of the variables was assessed both parametrically and using a randomisation test with 10,000 permutations (Manly, 1997).

2.4. Measuring seed production using seed traps around reproductive trees

We assessed the seed production by collecting seeds in seed traps. The number of viable seeds was subsequently calculated by multiplying the number of seed by their germination probability (in Section 2.6) to address the second objective of our study. Seed production was monitored for five reproductive trees of each species in each plot whenever possible, yielding a total of 18 *Cariniana* and 19 *Terminalia* trees >20 cm dbh. Seed traps (perforated umbrellas fixed upside down at the forest floor) with an area of 0.61 m^2 were placed around each tree in the distances 5, 10, 20, 30 and 35 m in the four cardinal directions. Only relatively isolated trees were selected for the study in order to avoid overlapping seed shadows, and traps were removed if the distance to a reproductive conspecific was <30 m. For trees ≤40 cm dbh the traps 30 m and 35 m from the tree were removed after eight weeks, as seeds apparently were not dispersed that far from small trees. Seeds were collected from the traps two times per month during the period when seeds were dispersed, i.e. from the beginning of July to mid-November 2002 (nine censuses). No seeds were dispersed outside this period (J. Justiniano and T. S. Fredericksen, pers. comm.).

Traps far from a seed tree captured a smaller proportion of the seeds dispersed to that distance, and the proportion captured decreased linearly with the distance. For each tree the 'relative' number of seeds R_c was therefore estimated by weighting the number of seeds in each trap by its distance to the tree, so $R_c = \sum_t S_{tc}(d_t + 1)$ where S_{tc} is the number of seeds in trap t in census c and d is the distance of the trap from the centre of the tree crown. This measure allows comparison of seed production among trees but does not give the absolute number of seeds produced by each tree. For missing traps S_{tc} was replaced by the mean number of

seeds collected in the other traps at that distance from the tree. A tree's seed production was calculated as the total number of seeds over the entire seed dispersal season. This number underestimated the real seed production for large *Cariniana* trees that were able to disperse seeds >35 m.

2.5. Assessing differences in seed germination and predation among trees and censuses

The viability of the collected seeds was tested by planting them in a shade-house at the end of each census (20 seeds per tree and census when available). Seeds were kept moist and trays with seeds from different trees and censuses were frequently shuffled around to ensure that they received the same amount of light. The germination time of each seed was recorded. Seeds that had not germinated 4 months after they were planted were considered dead. Parasitized, partly eaten seeds were counted separately in the field and not included in the analyses of seed viability.

The seed germination probability varied synchronously for all trees, so the germination probability of seeds from each tree and census was calculated as $P_{ci} = \bar{P}_c \bar{P}_i$, where $\bar{P}_i$ is the average germination probability for tree i, and $\bar{P}_c$ is the average germination probability in census c. This measure is less sensitive to the random death of a single seed than germination measured directly in the shade-house. After excluding three outliers the two germination measures correlated well ($r = 0.82$ for *Cariniana*; $r = 0.81$ for *Terminalia*). To analyse if seed germination differed among trees and censuses we used the log-linear model $\ln \hat{f}_{igc} = \mu + I_i + G_g + C_c + IG_{ig} + GC_{gc}$ where $\hat{f}$ is the expected frequency and G is germination status; see Crawley (2002) for details on the statistical model. The significance of $ICic$ and the three-way interaction could not be tested as not all trees dispersed seeds in all censuses.

Seed parasitism was only observed in *Terminalia*. In order to analyze whether the intensity of parasitism varied among censuses and trees we employed a G-test.

2.6. Assessing variations in production of viable seeds among reproductive trees

The effects of liana load, distance to conspecifics (NNI), number of competing neighbours and tree dbh on the number of viable seeds per tree were analyzed using generalized linear models (to address objective 3). The total number of viable seeds produced per reproductive tree over the season was calculated as $V = \sum P_c R_c$. The number of viable seeds produced by a tree in census c is the 'relative' number of seeds × germination probability. For one *Terminalia* too few seeds were planted to allow calculation of Pc. Instead the observed germination percentage was used for calculation of the number of viable seeds. Non-reproductive conspecifics were included in the calculation of NNI as many of them probably had flowers and could increase the amount of cross-pollination even though they did not produce any seeds. All variables were Log_e-transformed in order to obtain a linear relationship with $Log_e(V)$.

All statistical analyses were performed using R 2.6.1 (R Development Core Team, 2008), except regressions with permutation tests that were performed using Permute 3.4.9 (Legendre et al., 1994).

3. Results

3.1. Reproductive status of individual trees

The probability of producing seeds was related to liana load and tree diameter for both *Cariniana* and *Terminalia* (Table 1). The

Table 1
Change in reproductive status (whether trees produced seeds or not) with tree dbh, liana load (percent crown cover), distance to conspecifics (NNI, geometric mean of distance to two nearest conspecifics) and stand density (neighbours of all species >20 cm dbh <10 m away), calculated using logistic regressions.

Source	Estimate	SE	z	P_{par}	P_{ran}
Cariniana					
Intercept	−22.228	4.698	−4.731	<0.001	<0.001
Log_e(dbh)	6.708	1.283	5.229	<0.001	<0.001
Log_e(liana + 1)	−0.917	0.199	−4.607	<0.001	<0.001
Log_e(NNI)	−0.561	0.334	−1.680	0.093	0.002
Log_e(stand + 1)	−0.178	0.592	−0.301	0.763	0.156
Terminalia					
Intercept	−10.975	1.377	−7.969	<0.001	<0.001
Log_e(dbh)	3.406	0.368	9.269	<0.001	<0.001
Log_e(liana + 1)	−0.426	0.084	−5.094	<0.001	<0.001
Log_e(NNI)	0.042	0.193	0.215	0.829	0.462
Log_e(stand + 1)	0.248	0.272	0.912	0.362	0.908

Significance levels based on parametric tests P_{par} and on randomization tests P_{ran} are provided.

likelihood of producing seeds was lower for trees with a high liana load (Fig. 1). For *Cariniana* few of the trees with >20% of their crown covered by lianas were reproductive, whereas most *Terminalia* were reproductive as long as <80% of their crowns were covered. Very few trees <30 cm dbh produced any seeds (none of the 41 *Cariniana* trees, 22% of 186 *Terminalia*), whereas the large majority of the trees >80 cm dbh produced seeds (91% of 11 *Cariniana*, 91% of 22 *Terminalia*). Distance to nearest conspecifics (NNI) affected the reproductive status for *Cariniana* (Table 1), but the effect was only significant when the randomization test was used, indicating that there was strong spatial autocorrelation. The probability of producing seeds was slightly higher for trees that were far from conspecifics. The number of competing neighbouring trees had no effect on the reproductive status of *Cariniana* and *Terminalia*.

3.2. Seed germination and predation

For *Cariniana* 58% of the seeds germinated, usually <2 months after they were planted. A higher proportion of the seeds germinated at the peak of the seed dispersal season ($G^2 = 133.2$, d.f. = 16, $P < 0.001$) but there was no significant difference in germination among trees ($G^2 = 17.2$, d.f. = 10, $P = 0.07$), although the two trees where the smallest proportion of the seeds germinated (13% and 20%) had seeds that were infected by fungi throughout the seed dispersal season, and one of these trees was old and decaying.

Only 11% of the collected non-parasitized *Terminalia* seeds germinated. Germination times progressively decreased towards the end of the cold dry season, with seeds planted in the end of November germinating after <2 months. The proportion of seeds that germinated increased over the season ($G^2 = 205.9$, d.f. = 8, $P < 0.001$) and germination varied among trees ($G^2 = 105.5$, d.f. = 18, $P < 0.001$). The differences in seed germination among *Terminalia* trees were not related to liana load, NNI or dbh (GLM), and the average seed germination did not differ between trees in logged and reference plots.

A large part of the *Terminalia* seeds had been parasitized by bruchid beetles before dispersal, which left a small hole in the seed. The proportion of seeds that were parasitized dropped from 43% to 7% over the season (G-test; $G^2 = 843.9$, d.f. = 182, $P < 0.0001$). The intensity of the parasitism varied among trees ($G^2 = 1001$, d.f. = 173, $P < 0.0001$), and trees that were far from the nearest conspecifics were rarely parasitized ($R^2 = 0.35$, $P = 0.013$; regression with permutation test). Parasitism was not related to tree dbh, liana load or to number of seeds produced ($R^2 = 0.02$, $P = 0.94$).
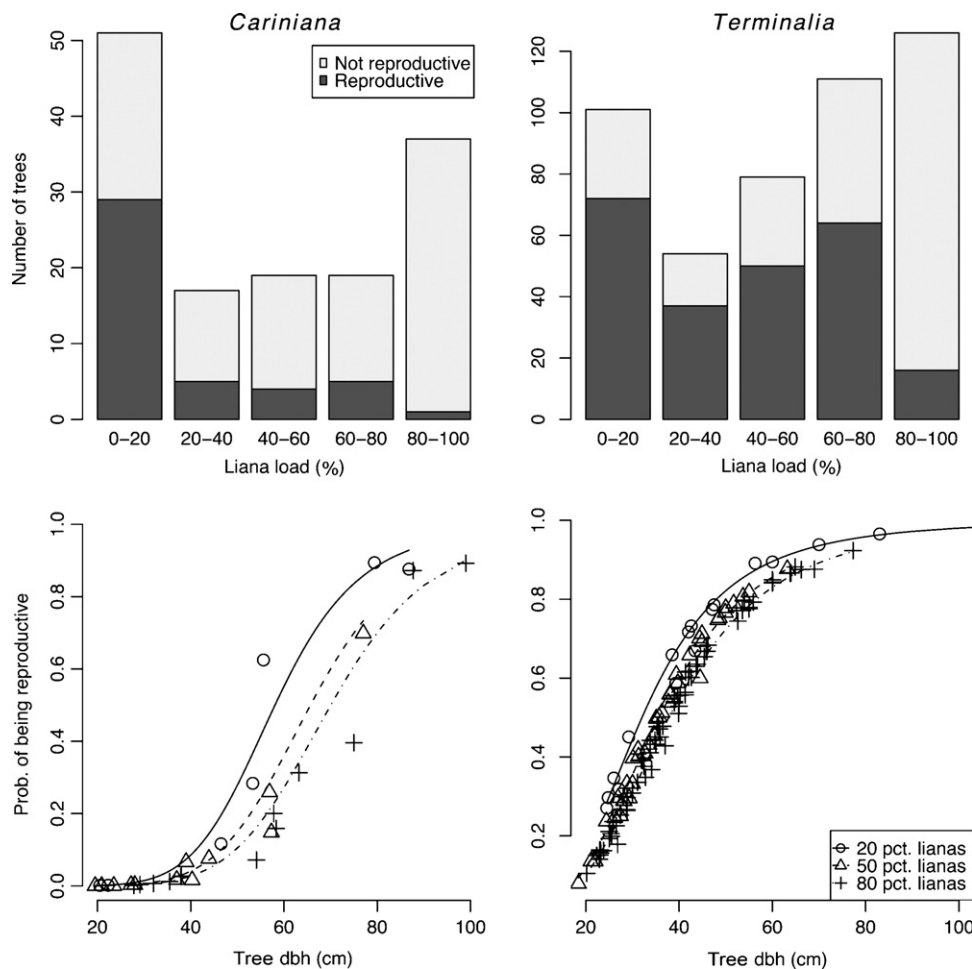
Fig. 1. Effect of liana load and tree diameter on the probability that trees produced seeds. Histograms show total number of trees in the four plots (intervals include upper limit). Curves show probability of producing seeds in three liana load classes, calculated from logistic regressions with dbh and liana load as independent variables. Points indicate predicted values corresponding to the full logistic model (Table 1).

3.3. Variation in number of viable seeds among reproductive trees

In *Cariniana* the number of viable seeds per seed tree was strongly related to liana load and tree diameter (Table 2; Fig. 2). The reproductive trees that had lianas in their crowns and trees with small diameter produced very few viable seeds, but the distance to nearest conspecifics and the number of competing trees did not affect seed production. In *Terminalia* the number of viable seeds per tree was not related to any of these variables (Table 2). There was no

consistent change in liana load with tree diameter, except that only relatively small trees had ≥90% liana cover in the studied species.

3.4. Total number of viable seeds in logged and unlogged areas

The total number of viable seeds was smaller in logged areas than in unlogged reference plots (Table 3). For *Cariniana* the

Table 2
Change in Log_e number of viable seeds with tree dbh, liana load, distance to conspecifics (NNI) and number of competing neighbours, calculated using GLM.

| Source	Estimate	SE	t	P
Cariniana				
Intercept	−8.665	3.293	−2.63	0.027
Log(dbh)	4.436	0.959	4.624	0.001
Liana load	−0.728	0.193	−3.765	0.004
Log(NNI)	−1.008	0.494	−2.042	0.072
Log(neighb)	−0.051	0.682	−0.074	0.942
Whole model: R^2 = 0.741				
Terminalia				
Intercept	14.619	6.247	2.34	0.036
Log_e(dbh)	−1.588	1.422	−1.117	0.284
Liana load	0.399	0.359	1.110	0.287
Log_e(NNI)	0.005	1.253	0.004	0.997
Log_e(neighb)	−2.304	1.534	−1.502	0.157
Whole model: R^2 = 0.227				
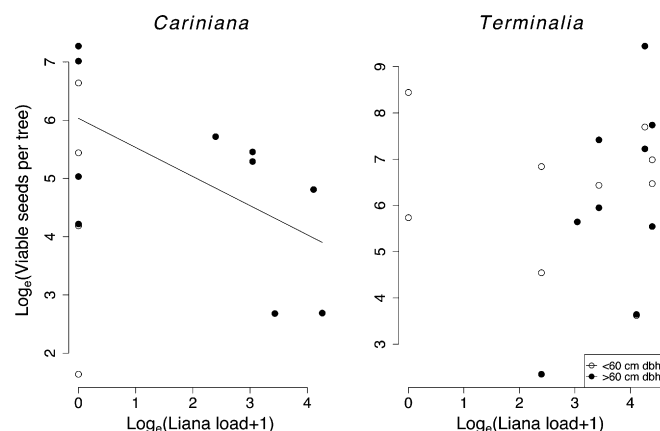
Fig. 2. Relationship between increasing liana load and number of viable seeds per tree for trees in the size classes ≤60 cm dbh and >60 cm dbh. Only the correlation for *Cariniana* >60 cm dbh was nearly significant (P = 0.07, $F_{1,8}$ = 4.3, R^2 = 0.35).

Table 3
Effects of selective logging on reproductive status, seed production and viability of *Cariniana ianeirensis* and *Terminalia oblonga* trees.

	Cariniana		Terminalia	
	Reference	Logged	Reference	Logged
Number of trees >20 cm dbh, N	108	40	262	321
Percent reproductive trees, q	31.5%	25.0%	47.7%	54.2%
Seeds per reproductive tree, $\overline{\sum R_c}$	932	147	11,333	3,443
Mean germination probability, $\overline{\sum P_c}$	56.9%	55.5%	10.8%	15.4%
Viable seeds per reproductive tree, $\overline{\sum P_c R_c}$	530	82	1,224	530
Total viable seeds, $qN\overline{\sum P_c R_c}$	18,020	820	153,000	92,220
Mean dbh ±1SD for trees >20 cm dbh	47.0 ± 22.0	45.5 ± 17.6	39.9 ± 16.9	41.8 ± 19.1
Trees with ≥20% liana load	68.0%	72.5%	84.4%	80.4%
Trees with ≥80% liana load	35.9%	32.5%	48.3%	37.3%
Number of trees harvested per ha	0	0.27	0	0.42
Proportion of trees >40 cm dbh harvested	0%	39%	0%	12%
Mean dbh ±1SD of harvested trees		76.5 ± 15.6		60.9 ± 7.9

The total relative number of viable seeds produced by all trees in two 450-m × 600-m plots was calculated assuming that the studied seed trees were representative of all reproductive trees. The relative number of seeds strongly underestimates the true seed production, but scales among trees in the same way. Over-bars indicate mean values for the studied seed trees. Logging caused smaller decreases in tree density for *Terminalia* than for *Cariniana* (IBIF unpubl. data).
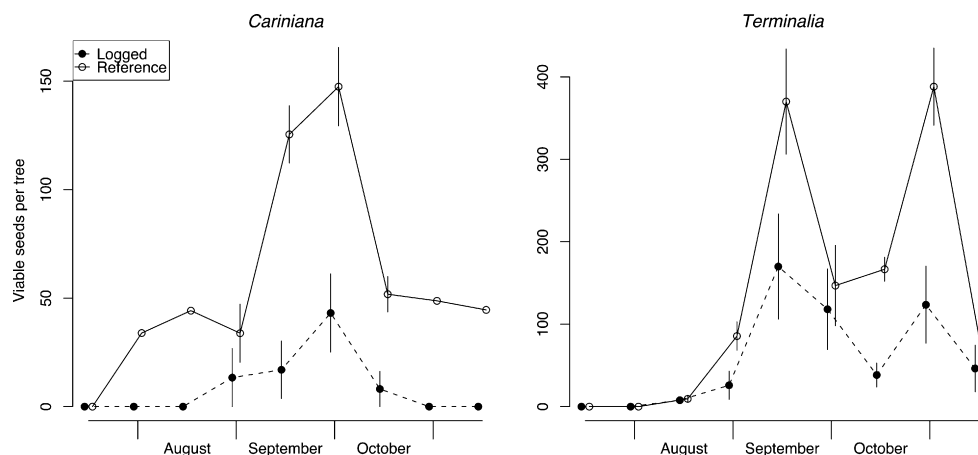

Fig. 3. Variation in mean number of viable seeds per reproductive tree in *Cariniana ianeirensis* and *Terminalia oblonga* (mean ± 1SE). The two peaks in the seed dispersal for *Terminalia* results from variations in number of seeds dispersed rather than in seed viability, which increased monotonously over the study period.

decrease was caused by a combination of a strongly reduced number of seed trees and a very limited seed production on the trees that were left. For *Terminalia* the difference between logged and reference plots was small and mostly due to one single tree in a reference plot that produced 45% of all collected seeds (but only 21% of collected viable seeds). Only a small proportion of the *Terminalia* had been logged in the studied plots. The production of viable seeds peaked at the same time in logged and reference plots (Fig. 3).

4. Discussion

In *Cariniana* and *Terminalia* the largest trees and trees with small liana loads had a higher probability of producing seeds, whereas distance to conspecifics and number of competing trees had no effect on their reproductive status. *Cariniana* was particularly strongly affected by lianas, and the majority of the trees that had more than 20% of their crowns covered by lianas did not produce seeds. On Barro Colorado Island (BCI), Panama, five of 16 tree species were less frequently fertile when covered by lianas (Wright et al., 2005), presumably due to competition for light. In *Cariniana* the liana-covered fertile trees at the same time produced fewer seeds, which amplified the negative impact of lianas. Similar relationships between liana load and number of seeds produced

have, to our knowledge, only been reported for the trees *Bursera simaruba* in Costa Rica (Stevens, 1987) and for *Bertholletia excelsa* in Brazil (Kainer et al., 2006).

Lianas may generally have a strong impact on tree fertility because of their ability to grow fast and to position their leaves on top of the tree crowns, thereby causing significant reductions in the amount of light that is available to the trees (Putz, 1984; Grauel and Putz, 2004). Kainer et al. (2006) suggested that liana-infested trees may also experience reduced nutrient availability, as leaves that are less exposed transpire less and transport less water and minerals. Although lianas grow fast they probably need >1 year to fully exploit a new logging gap. Their densities are therefore likely to have increased further in the logged plots in La Chonta after this study took place, which may have increased their negative effects on tree reproduction.

Similar mechanisms are likely to be responsible for the decreased reproduction in *Cariniana* and *Terminalia*, but the reason why reproduction is not affected to the same extent in the two species is less clear. *Terminalia* experienced higher liana loads than *Cariniana* (Table 3), probably because of its Y-shaped architecture and its lower height to the first branches. Consequently, we speculate that a generally higher liana load on *Terminalia* has made it particularly beneficial to evolve the ability to produce seeds even when covered by lianas. This hypothesis is supported by the fact

that *Terminalia* growth rates are less affected by liana infestation (0.28 cm y^{-1} and 0.17 cm y^{-1} for liana-free trees and trees entirely covered by lianas, respectively) than are *Cariniana* growth rates (0.68 cm y^{-1} and 0.17 cm y^{-1}; IBIF unpubl. data). The five tree species on BCI that produced seeds less often when liana infested varied in life forms (Wright et al., 2005), and it is not clear if the species that were most strongly affected by lianas were the ones that were least susceptible to being infested. If lianas have a larger impact on reproduction in trees that rarely host lianas, it would help focussing silvicultural treatments like liana removal on the species where it has the largest impact.

Cariniana and *Terminalia* did not produce nearly as many viable seeds in logged forest as compared with the reference plots. This was apparently not due to lower levels of cross-pollination for trees that were further apart, as the distance between neighbouring trees had no significant effect on the probability of seed germination or on the total number of viable seeds produced per tree in either species. A similar result was obtained by Herrerias-Diego et al. (2006) who found no effect of forest fragmentation on the level of outcrossing. Lourmas et al. (2007) reported that average pollination distances exceeded 250 m in the bee-pollinated *Entandrophragma cylindricum*, suggesting that logging may have a weak effect on the outcrossing levels in tropical trees as long as post-logging densities remain high. In our study, there was instead evidence of distance-dependent seed predation by bruchid beetles in *Terminalia* and of an increasing probability of producing seeds for *Cariniana* trees that were far from conspecific neighbours (Table 1). These trends serve to reduce the negative effects of logging on seed production but they were not able to compensate completely for the reduction in number of seeds produced (Table 3).

The reduced seed production in logged forest may partly be caused by alterations of forest structure induced by logging, although such changes were not easily perceived in La Chonta. Selective logging often results in reduced canopy heights (Okuda et al., 2003; Blate, 2005; Dietz et al., 2006; Villela et al., 2006), which may lead to increased transpiration of the remaining large trees (Laurance et al., 2000) and reduce their seed production. Alternatively the fruits and seeds may be more visible in the logged forest, which could make them more exposed to predation by birds. Our results indicate that there can be variation in seed viability among trees and that seeds from healthy trees may be more viable. Another possible reason for the lower average seed production in logged areas could therefore be that all the large, healthy and more fecund trees had been logged, which would have a detrimental long-term impact on forest regeneration. This must be taken into account when selecting the individuals that should be left as seed trees when logging takes place.

5. Conclusion

The intensive logging of *Cariniana*, combined with a lower average seed set on the remaining trees means that the species contributed much less to the total seed production in logged than in unlogged forest stands. This is expected to result in long-term changes of the species composition, thus rendering logging unsustainable unless regeneration is improved through silvicultural treatments (Dalling et al., 2002; De Steven and Wright, 2002). Our results indicate that seed production can be substantially improved in *Cariniana* by cutting lianas on the seed trees. If lianas were removed on the relatively abundant trees with 50–70 cm dbh, it could result in a 50–100% increase in the number of reproductive trees (Fig. 1), and in a considerable increase in the number of viable seeds produced per tree (Fig. 2). Liana-cutting experiments have revealed that

the effects of removing lianas persist for at least 4 years in La Chonta (Peña-Claros et al., 2008). Liana cutting may therefore be a relatively cost effective way of improving regeneration of trees with poor seed production.

References

Alvira, D., Putz, F.E., Fredericksen, T.S., 2004. Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia. For. Ecol. Manage. 190, 73–86.

Augspurger, C.K., 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. J. Ecol. 71, 759–772.

Blate, G.M., 2005. Modest trade-offs between timber management and fire susceptibility of a Bolivian semi-deciduous forest. Ecol. Appl. 15, 1649–1663.

Campanello, P.I., Garibaldi, J.F., Gatti, M.G., Goldstein, G., 2007. Lianas in a subtropical Atlantic Forest: host preference and tree growth. For. Ecol. Manage. 242, 250–259.

Cintra, R., 1997. A test of the Janzen–Connell model with two common tree species in Amazonian forest'. J. Trop. Ecol. 13, 641–658.

Clark, D.A., Clark, D.B., 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen–Connell model. Am. Nat. 124, 769–788.

Clark, D.B., Clark, D.A., 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. J. Trop. Ecol. 6, 321–331.

Crawley, M.J., 2002. Statistical Computing: An Introduction to Data Analysis Using S-Plus. John Wiley & Sons, Chichester, UK.

Dalling, J.W., Muller-Landau, H.C., Wright, S.J., Hubbell, S.P., 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. J. Ecol. 90, 714–727.

De Steven, D., Wright, S.J., 2002. Consequences of variable reproduction for seedling recruitment in three neotropical tree species. Ecology 83, 2315–2327.

Dietz, J., Holscher, D., Leuschner, C., Hendrayanto, 2006. Rainfall partitioning in relation to forest structure in differently managed montane forest stands in Central Sulawesi, Indonesia. For. Ecol. Manage. 237, 170–178.

Eriksson, O., Ehrlen, J., 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91, 360–364.

Fredericksen, T.S., Mostacedo, B.M., Justiniano, M.J., Ledezma, J., 2001. Seed tree retention considerations for uneven-aged management in Bolivian tropical forests. J. Trop. For. Sci. 13.

Fredericksen, T.S., Pariona, W., 2002. Effect of skidder disturbance on commercial tree regeneration in logging gaps in a Bolivian tropical forest. For. Ecol. Manage. 171, 223–230.

Gentry, A.H., 1993. A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru) – with Supplementary Notes on Herbaceous Taxa. Conservation International, Washington, DC.

Gerwing, J.J., 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. J. Appl. Ecol. 38, 1264–1276.

Ghazoul, J., Liston, K.A., Boyle, T.J.B., 1998. Disturbance-induced density-dependent seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. J. Ecol. 86, 462–473.

Ghazoul, J., McLeish, M., 2001. Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. Plant Ecol. 153, 335–345.

Grauel, W.T., Putz, F.E., 2004. Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. For. Ecol. Manage. 190, 99–108.

Guariguata, M.R., 1999. Early response of selected tree species to liberation thinning in a young secondary forest in Northeastern Costa Rica. For. Ecol. Manage. 124, 255–261.

Hall, P., Walker, S., Bawa, K.S., 1996. Effect of forest fragmentation on genetic diversity and mating system in a tropical tree, *Pithecellobium elegans*. Conserv. Biol. 10, 757–768.

Herrerias-Diego, Y., Quesada, M., Stoner, K.E., Lobo, J.A., 2006. Effects of forest fragmentation on phenological patterns and reproductive success of the tropical dry forest tree *Ceiba aesculifolia*. Conserv. Biol. 20, 1111–1120.

Kainer, K.A., Wadt, L.H.O., Gomes-Silva, D.A.P., Capanu, M., 2006. Liana loads and their association with *Bertholletia excelsa* fruit and nut production, diameter growth and crown attributes. J. Trop. Ecol. 22, 147–154.

Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H.L., Lovejoy, T.E., 2000. Rainforest fragmentation kills big trees. Nature 404, 836.

Laurance, W.F., Pérez-Salicrup, D.R., Delamônica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L., Lovejoy, T.E., 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82, 105–116.

Legendre, P., Lapointe, F.-J., Casgrain, P., 1994. Modeling brain evolution from behavior: a permutational regression approach. Evolution 48, 1487–1499.

Lourmas, M., Kjellberg, F., Dessard, H., Joly, H.I., Chevallier, M.H., 2007. Reduced density due to logging and its consequences on mating system and pollen flow in the African mahogany *Entandrophragma cylindricum*. Heredity 99, 151–160.

Manly, B.F.J., 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. Chapman & Hall, London.

Mori, S.A., Boeke, J.D., 1987. Chapter XII. Pollination. Mem. N.Y. Bot. Gard 44, 137–155.

Mostacedo, B.M., Fredericksen, T.S., 1999. Regeneration status of important tropical forest tree species in Bolivia: assessment and recommendations. For. Ecol. Manage. 124, 263–273.

Nabe-Nielsen, J., Severiche, W., Fredericksen, T.S., Nabe-Nielsen, L.I., 2007. Timber tree regeneration along abandoned logging roads in a tropical Bolivian forest. New For. 34, 31–40.

Okuda, T., Suzuki, M., Adachi, N., Quah, E.S., Hussein, N.A., Manokaran, N., 2003. Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia. For. Ecol. Manage. 175, 297–320.

Pariona, W., Fredericksen, T.S., Licona, J.C., 2003. Natural regeneration and liberation of timber species in logging gaps in two Bolivian tropical forests. For. Ecol. Manage. 181, 313–322.

Peña-Claros, M., Peters, E.M., Justiniano, M.J., Bongers, F., Blate, G.M., Fredericksen, T.S., Putz, F.E., 2008. Regeneration of commercial tree species following silvicultural treatments in a moist tropical forest. For. Ecol. Manage. 255, 1283–1293.

Prance, G.T., Mori, S.A., 1979. Lecythidaceae. Part I. Flora. Neotrop. Monogr. 21, 1–270.

Putz, F.E., 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65, 1713–1724.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Schiøtz, M., Boesen, M.V., Nabe-Nielsen, J., Sørensen, M., Kollmann, J., 2006. Regeneration in *Terminalia oblonga* (Combretaceae) — A common timber tree from a humid tropical forest (La Chonta, Bolivia). For. Ecol. Manage. 225, 306–312.

Snook, L.K., Camara-Cabrales, L., Kelty, M.J., 2005. Six years of fruit production by mahogany trees (*Swietenia macrophylla* King): patterns of variation and implications for sustainability. For. Ecol. Manage. 206, 221–235.

Stevens, G.C., 1987. Lianas as structural parasites: the *Bursera simaruba* example. Ecology 68, 77–81.

Villela, D.M., Nascimento, M.T., Aragão, L.E.O.C., da Gama, D.M., 2006. Effect of selective logging on forest structure and nutrient cycling in a seasonally dry Brazilian Atlantic forest. J. Biogeo. 33, 506–516.

Wright, S.J., Jaramillo, M.A., Pavon, J., Condit, R., Hubbell, S., Foster, R., 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. J. Trop. Ecol. 21, 307–315.