Growth responses of neotropical trees to logging gaps

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Summary

1. Modelling growth strategies among tropical trees is an important objective in predicting the response of tree dynamics to selective logging and in gaining insights into the ecological processes that structure tree communities in managed tropical forests.

2. We developed a disturbance index to model the effects of distance to and area of logging gaps on stem radial growth rates. This index was tested using census data of 43 neotropical tree species, representing a variety of life-history strategies and developmental stages, from a selectively logged forest at Paracou, French Guiana. Growth strategies were analyzed in light of two indicators: the inherent species growth rate (when disturbance index is null) and the species reaction (change in growth rate) to logging gaps.

3. Across species, the predicted inherent growth rates in unlogged forest ranged from 0·25 to 6·47 mm year^{-1}, with an average growth of 2·29 mm year^{-1}. Ontogenetic shifts in inherent growth rate were found in 26 of the 43 species.

4. Species growth response to logging gaps varied widely among species but was significantly positive for 27 species. The effect of ontogeny on growth response to logging was retained for 14 species, and species with inherent fast growth rate (5 mm year^{-1}) responded less to logging gap disturbances than did species with slow inherent growth (1 mm year^{-1}).

5. Functional traits explained 19–42% of the variation in the inherent growth rate and in species' response across all developmental stages. Whereas maximum diameters and seed mass were strong predictors of inherent growth rate, maximum height, wood density, mode of germination and stem architecture were additionally involved in tree growth response.

6. *Synthesis and applications*: This study provides a necessary framework for developing predictive post-logging growth models for the thousands of species comprising tropical forests and is sufficiently general to apply to a broad range of managed tropical forests.

Key-words: canopy openings, functional traits, incidence function model, light partitioning, selective logging, tree growth rates, tropical rain forest

Introduction

The description of growth strategies among tropical forest tree species remains an important objective in tropical forest management to determine timber yield and long-term response of forest structure and dynamics to selective logging (Finegan, Camacho & Zamora 1999; Peña-Claros *et al.* 2008; Chazdon *et al.* 2010). Although lowland Amazonian forests often contain more than 150 species per hectare (Ter Steege *et al.* 2003), with dozens of commercially valuable timber species (Gourlet-Fleury, Guehl & Laroussinie 2004), to date research efforts

have focused on the post-logging demography of comparatively few species. Not only are data for a larger number of species still needed, but an approach to generalize these results to species for which data are not available would also prove valuable.

Logging gaps create canopy openings that expose understorey trees to sunlight of increased duration and intensity (Asner, Keller & Silva 2004). To date, most work on the differential response of tree species to light gradients has examined juvenile stages (Poorter 1999; Baraloto, Goldberg & Bonal 2005), both because assembling sufficient data for adults of many species requires plots of tens of hectares and multiple censuses due to slow diameter growth (Clark & Clark 2001; Wagner *et al.* in

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press), and because it remains difficult to define light environments of individual trees (Poorter *et al.* 2005; King *et al.* 2006). Studies addressing differential response to light among larger trees have used approximations based on neighbourhood competition, nearby canopy area or some definition of a canopy illumination index (Clark & Clark 1999; Hubbell *et al.* 1999; Keller *et al.* 2004; Uriarte *et al.* 2004b). To our knowledge, no study has modelled the individual tree growth response using a spatially explicit index of logging gap induced disturbance.

A further complication in modelling tree growth arises because growth strategies may change with ontogeny, i.e. with the development history of a tree within its own lifetime (Clark & Clark 1999; Poorter *et al.* 2005). The prevalence of ontogenetic shifts in growth across a large number of tropical tree species remains unknown, as do interactions between ontogeny and light availability on growth rates. A high abundance of such shifts would profoundly change our current views on the role of disturbance in the dynamics of tropical tree communities (Hubbell *et al.* 1999) and, consequently, sustainable management for timber extraction.

Traditionally, forest modellers have simplified the large number of tropical tree species into groups using criteria that include taxonomic affinity, ecological guilds or similar growth curves (Vanclay 1991) to model post-logging forest dynamics. Still lacking are solutions to (i) predict the responses of species for which direct growth measurements are lacking and (ii) extrapolate growth models found in long-term forest plots to forest areas with no census data. One promising solution employs tree functional traits as a proxy of tree growth strategies (Poorter *et al.* 2008), defined here as the combination of tree inherent growth rates and tree reaction to canopy gaps. These traits are now well-recognized as reliable criteria to predict species performance, distribution or abundance across diverse environmental gradients (Herault & Honnay 2007) because they are directly linked to the species vital rates (survival, growth and reproduction efficiency) and thus fitness (McGill *et al.* 2006; Sterck, Poorter & Schieving 2006; Herault 2007). Given that large trait data bases on tropical trees are now emerging (Ollivier, Baraloto & Marcon 2007; Baraloto *et al.* 2010), testing and demonstrating the ability of functional traits to accurately predict growth behaviour could have important implications for developing, in the future, robust post-logging models in tropical forests.

Here, we present a unique data set from a selectively logged forest and apply to it a novel spatially explicit approach using a disturbance index that fully integrates the distance of individual stems from neighbouring logging gaps of different sizes. Logging has resulted in a spatially complex mosaic of canopy openings that vary in size and shape. This experimental design offers the opportunity to model both inherent stem radial growth rates and stem radial growth responses to logging gaps using appropriate spatial statistics. Stem radial growth rates represent an integrative measure of tree vigour and tree response to logging, are the most commonly measured variable in long-term forest plots, and are widely used in individual-based forest simulators to model post-logging tree growth and

thus to support forest management (Gourlet-Fleury & Houllier 2000). Our data set includes stem growth data for large populations of 43 tree species, including a broad range of size classes of adult trees. Across these species, life-history traits have been measured, permitting a rigorous test of the predictive power of these traits to explain inherent growth rate and growth response to logging gaps (Poorter *et al.* 2008).

Materials and methods

STUDY SITE

The study was conducted at the Paracou experimental site (5°18′N, 52°55′W), a lowland tropical rain forest near Sinnamary, French Guiana. The site receives nearly two-thirds of the annual 3041 mm of precipitation between mid-March and mid-June, and < 50 mm per month in September and October (Gourlet-Fleury, Guehl & Laroussinie 2004). More than 550 woody species attaining 2 cm DBH (diameter at breast height) have been described at the site, with 150–180 species of trees ≥10 cm DBH per hectare. The floristic composition is typical of Guianan rainforests (Ter Steege *et al.* 2003) with dominant families including Leguminoseae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae.

In 1984, 12 plots of 6·25 ha each were established at the Paracou site for a complete annual inventory of all trees ≥10 cm DBH. From October 1986 to May 1987, the plots underwent three logging treatments, with three plots assigned as controls. An average of 10 trees ≥50 or 60 cm DBH (treatment 1, 3 plots), 32 trees ≥40 cm DBH (treatment 2, 3 plots) and 40 trees ≥40 cm DBH (treatment 3, 3 plots) were removed per hectare. Three new additional control plots of 6·25 ha were established in 1990.

SAMPLING AND MEASUREMENTS

This study made use of three data sets collected from the site. First, all trees ≥10 cm in DBH (diameter at 1·3 m height) have been mapped and measured annually from 1984 to 1995 and every 2 years thereafter in fifteen 6·25 ha permanent plots (Gourlet-Fleury, Guehl & Laroussinie 2004; Rutishauser *et al.* in press). We examined growth for 7176 trees of the 43 species having at least 30 individuals that were (i) not damaged during logging operations, (ii) located at least 5 m from skidtrails and (iii) not buttressed because we were not confident on the height of the initial DBH measures for these trees. Annual growth rates (AGRs) were calculated from complete forest inventories conducted in 1988 and 1992 directly after artificial gaps were created by logging activity. We chose to study tree growth during the 4-year post-logging period because most of the additional tree growth arises immediately after logging (Okuda *et al.* 2003).

Second, a geographic information system (GIS) spatial data base was constructed using detailed maps drawn by logging teams at the time of harvesting activities. Areas of logging gap due to tree felling were projected to the ground surface and were converted to an ArcGIS (ESRI, Redlands, CA, USA) shapefile. Harvest gap area in the logged plots averaged 27·8% of forest area. In total, 405 forest gaps (averaging 28 gaps ha^{-1}) were artificially created by forest exploitation.

Third, information on seven functional traits for which (i) information was available for the 43 focal species and (ii) trait values do not change with ontogeny, was extracted from a trait data base (Appendix S1) developed for the Guiana Shield region (Digital Appendix A,Ollivier, Baraloto & Marcon 2007). These seven key-traits have been often proposed to be important for plant performance and to

represent complementary axes of tree ecological strategies in tropical forests (Westoby 1998; Weiher *et al.* 1999; Poorter *et al.* 2008): tree position in forest layers and stem architecture play a pivotal role in access to light, height and DBH at tree maturity indicate the place for volume expansion in tree bole, wood density represents the biomass invested per unit wood volume, and seed mass and seedling morphology influence reproduction, dispersal and establishment. Complete details on the methods used to estimate trait values are given in Appendix S1.

STATISTICAL ANALYSES

The effects of logging gaps on the growth of rainforest trees are often difficult to quantify properly due to the complex spatial configuration of the induced disturbances. In this study, we used a model inspired from the metapopulation incidence function model (Hanski 1994) to quantify the effects of distance to (modelled as an exponential decay) and area of (modelled in a power function) logging gaps on individual growth. In a first step, we parameterize the disturbance index by minimum least square, and estimated parameters' uncertainty with a residual bootstrap procedure (Efron & Tibshirani 1993), using both undetermined individuals as well as individuals belonging to species having < 30 records in our data set (7453 records). We choose to use this independent data set to increase the robustness (and thus the transposability) of our conclusions with fewer circularity problems.

$$AGR_i = \mu \times \sum_i^j \left(e^{-a \times \text{Distance}_{ij}} \times \text{Surface}_j^\beta \right) + \varepsilon_i$$

$$AGR_i = \mu \times \text{Idisturb}_i + \varepsilon_i \quad \text{with } \varepsilon \sim N(0, \sigma^2),$$

where AGR is the annual growth rate of the individual i, Distance is the edge-to-tree distance between logging gap j and individual i, and Surface is the surface area in m^2 of logging gap j. μ, α and β were the disturbance index parameters. Note that when, respectively, α or β equal zero, the effect of distance to or area of logging gap on tree growth is null.

The second step was to explicitly test the effect of logging gap and developmental stage on species growth rates of each focal species. We first allocated a disturbance index (Idisturb) to all individuals belonging to the 43 focal species using the parameter α and β found during the first step. This individual disturbance index was used in predictive models of species growth rate including (i) the degree of soil hydromorphy (Soil), *terra firme* or not (Baraloto *et al.* 2007); (ii) the level of local competition (Comp), computed using data from the year immediately preceding logging and estimated as the stand basal area of all trees in a circular neighbourhood of 200 m^2 around each focal tree; and (iii) the tree size effect, for which we used the ratio between the individual DBH and the 95th percentile (see King, Davies & Noor 2006) of the DBH values in the species' population across all unlogged plots at Paracou. In the final growth model, we introduced both the ratio and the squared ratio to obtain a flexible enough mathematical form allowing a monotonically increasing, a monotonically decreasing or a humped growth. The final growth model was constructed for each focal species as:

$$
\begin{aligned}
AGR_i =\ & \mu \times \text{Idisturb}_i + \delta \times \text{Soil}_i + \theta \times \text{Comp}_i \\
& + \lambda \times \frac{\text{DBH}_i}{\text{DBH95}} + \gamma \times \left(\frac{\text{DBH}_i}{\text{DBH95}} \right)^2 \\
& + \rho \times \text{Idisturb}_i \times \frac{\text{DBH}_i}{\text{DBH95}} + \omega + \varepsilon_i \quad \text{with } \varepsilon \sim N(0, \sigma^2),
\end{aligned}
$$

where AGR is the annual growth rate of the individual i of the focal species; μ, δ, θ, λ, γ, ρ and ω are the fitted-model parame-

ters; and ε the fitted-model residuals. The interaction parameter ρ was introduced in the model because we explicitly tested the hypothesis of a differential growth response to logging gaps with ontogeny.

Species growth responses to logging gaps depend on two estimable factors: the inherent species growth rate and the species reaction (change in growth rate) to logging gap. Estimates of these two factors can easily be derived from each specific AGR model. First, inherent growth rates were calculated as the predicted intercepts (ω) of each specific AGR model and is defined as the mean-specific growth in undisturbed areas (Idisturb = 0) and in a moderate competition (Comp = 28·8 m^2 ha^{-1}, i.e. the averaged individual tree value on the whole data set). Secondly, reactions to logging gaps were calculated as the predicted slopes against the disturbance index of the specific growth models (μ). But we need to acknowledge that both intercepts and slopes are dependent (at least for some species) on the developmental stage (i.e. corrected by ρ, λ, γ) and that the interpretation of these coefficients is difficult unless we reduce ontogeny to ordinal classes. We thus chose to derive three sets of predicted slopes and intercepts, corresponding to three representative developmental stages (DBH/DBH95 cutoffs of 0·4 [hereafter juvenile], 0·6 [young adult] and 0·8 [adult]).

To explore the relationships between inherent growth rates and species reaction to logging gaps, we performed an analysis of covariance where the three developmental stages were coded as qualitative factors. We then investigated the extent to which the seven functional traits can be used to predict species inherent growth rates and growth response to logging gaps, building a general linear model for each of the two predicted variables (inherent growth or growth response to canopy gaps), at each of the three developmental stages (juvenile, young adult and adult).

Throughout the data analysis, the Akaike Information Criterion (AIC) was always used in a stepwise algorithm to choose the most parsimonious models and to avoid over-parameterization (Legendre & Legendre 1998). All analyses were performed using the R project software (http://www.r-project.org/).

Results

The parameterization of the disturbance index by minimum least square led to $\alpha = 0{\cdot}107 \pm 0{\cdot}03$ and $\beta = 0{\cdot}258 \pm 0{\cdot}04$, suggesting that the gap opening affected tree growth at very low distances (< 10 m) and that the effect of increasing gap area on tree growth is weaker (see Fig. 1).

The breadth of specific inherent growth rates, estimated as the predicted intercepts of each specific growth model for the three investigated ontogenical stages, for a disturbance index set to 0 and for a competition index set to 28·8 (averaged competition index value across the entire data set), ranged from 0·26 (adult *Licania sprucei*) to 6·47 (adult *Eschweilera coriacea*) and averaged 2·30 ± 1·44 mm year^{-1}. The effect of ontogeny on the inherent growth rate (λ and γ) was found in 26 species (Table 1): 11 species having slower growth with increasing tree size (negative λ or negative γ with no retained λ), 7 species exhibiting faster growth with increasing size (positive λ), 8 species exhibiting a typical hump-shaped curve (positive λ and negative γ; Figs 2a and b) and the last 4 species exhibiting an atypical hump-shaped curve (negative λ and positive γ).
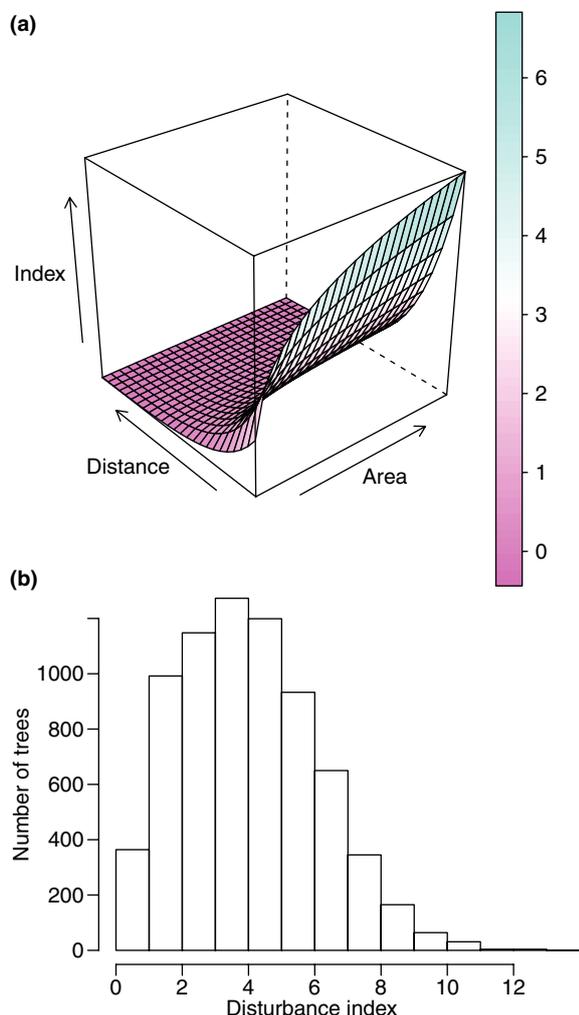
(a)

(b)

Fig. 1. The mathematical behaviour of the disturbance index across a realistic range of area of (X axis, 0–2000 m^2) and distance to (Y axis, 0–50 m) logging gaps (a) and histogram of the obtained values for the 7453 individual trees used for parameterization of the disturbance index (b).

Growth was affected by logging gaps for 30 species (μ retained in the final model). The average growth response to logging gaps, estimated as the predicted slopes against the disturbance index for the three investigated ontogenical stages of the 43 species, was positive (0·12 ± 0·24), indicating that, at the community level, tree individual growth increased with proximity of a logging gap. However, the value of the standard deviation also indicated that the variation of responses was very high with a minimum value of −0·79 (adult *Eschweilera decolorans*) and a maximum of 0·73 (adult *Virola michelii*). The effect of ontogeny on the growth response to disturbance was found for 14 of the 43 species (ρ retained in the final model). Ten species showed increased growth near logging gaps when juveniles and a decreasing growth when adults (Fig. 2d), with the four others having the opposite behaviour.

Analysis of covariance indicated a strong negative correlation between inherent growth rates and species growth response ($P \leq 0.01$; Fig. 3). In other words, species with inherent fast growth exhibited less reaction to logging gaps than did species with slower inherent growth. Moreover, we detected significantly different slopes ($P \leq 0.05$) with a tendency for a more marked reduction in growth response to logging gaps for faster-growing species when older (Fig. 3).

Functional traits explained between 28% and 35% of variation in the inherent growth rate across all developmental stages and between 19% and 42% of the variation in species' response to increasing disturbance (Table 2). Whereas maximum DBH and seed mass were, respectively, the first and second predictors of inherent growth rate and growth response, models of growth response retained three additional and important predictors: stem architecture, mode of germination and wood density.

Discussion

Whereas several previous studies have described differential growth strategy of tropical trees for species groups (Vanclay 1991; Gourlet-Fleury & Houllier 2000) or for a rather limited set of species (e.g. Clark & Clark 1999), our results represent one of the first studies of tree-specific growth rate responses to logging gaps for a large set of species. The range of species inherent growth rates we observed for trees > 10 cm in DBH (0·25–6·47 mm year^{-1}) encompasses almost the entire range reported in other cross-habitat studies in Costa Rica (0·5–6·7 mm year^{-1}; Clark & Clark 1999; Lieberman & Lieberman 1985), Bolivia (0·2–2·7 mm year^{-1}; Brienen & Zuidema 2006) and Malaysia (0·6–6·1 mm year^{-1}; King *et al.* 2006).

The quality of the fit of our specific models was highly variable (Table 1, Appendix S2). Overall, they showed similar or enhanced explanatory power relative to other models developed to (i) analyze neighbourhood influence (Uriarte *et al.* 2004a), (ii) investigate soil influences on tropical tree growth (Russo *et al.* 2008) or (iii) to include the effects of topography in the same forest (Baraloto *et al.* 2007). Nevertheless, a substantial fraction of individual variation in growth remains unexplained. Tree growth is influenced by several non-investigated additional environmental variables (topography, light availability, etc.) and also by the unique individual history that depends on complex environmental changes occurring before logging (Uriarte *et al.* 2004a).

INHERENT-SPECIFIC GROWTH RATES

By the nature of our analysis, we include *a priori* the possibility that trees may change their inherent growth with developmental stages (λ and γ). Basically, three strategies may be possible: increasing, decreasing or having a humped inherent growth rates with ontogeny. The three strategies were not equally distributed among the 26 of 43 species that show such an ontogenic shift. Most species (11) showed decreasing growth. These trees are abundant understorey trees rarely receiving direct light and having low DBH95. This means that they were mainly sampled at high DBH/DBH95 ratio, i.e. rather close to senescence. It is thus possible that they have followed a hump-backed curve but with a growth peak below 10 cm DBH. Among the seven species for which growth increases with

Table 1. Effects of logging gaps and developmental stage on the growth rates of 43 tropical trees, Akaike Information Criterion used to choose the most parsimonious specific model

Species	μ	λ	γ	ρ	θ	ω	P	R^2
Andira coriacea	0·70 ± 0·31					0·97 ± 1·47	*	0·14
Bocoa prouacensis	0·30 ± 0·12	0·91 ± 0·92				0·82 ± 0·54	**	0·04
Catostemma fragrans	0·24 ± 0·08			-0·40 ± 0·21		0·47 ± 0·35	**	0·10
Carapa procera	0·76 ± 0·36	3·90 ± 3·07		-0·99 ± 0·68		1·55 ± 1·68	*	0·07
Chaetocarpus schomburgkianus	0·13 ± 0·09					1·54 ± 0·40	ns	/
Couratari multiflora	0·29 ± 0·09					0·83 ± 0·39	**	0·10
Dicorynia guianensis	0·48 ± 0·20	16·94 ± 5·00	-10·80 ± 4·38	-0·76 ± 0·43		-0·76 ± 1·35	**	0·11
Eperua falcata	0·22 ± 0·06		-1·49 ± 0·46		-0·61 ± 0·40	3·29 ± 0·36	***	0·07
Eperua grandiflora	0·29 ± 0·08	21·93 ± 5·16	-24·49 ± 5·79			-0·46 ± 1·01	***	0·17
Eschweilera coriacea	0·75 ± 0·33	22·17 ± 6·64	-12·47 ± 4·33			-3·16 ± 2·20	*	0·06
Eschweilera decolorans	2·26 ± 0·48	6·97 ± 2·46		-1·77 ± 0·66		-1·69 ± 1·44	***	0·43
Eschweilera sagotiana	0·14 ± 0·03	-0·97 ± 0·29		-3·82 ± 0·87		1·76 ± 0·20	***	0·04
Eschweilera congestiflora						2·20 ± 0·19	ns	/
Goupia glabra						3·53 ± 0·41	ns	/
Gustavia hexapetala	1·26 ± 0·40	-2·07 ± 0·51				2·53 ± 0·35	***	0·09
Hebepetalum humirifolium	0·24 ± 0·15	-4·75 ± 6·27	8·07 ± 5·09	-1·96 ± 0·73		2·39 ± 2·16	**	0·27
Hevea guianensis						1·51 ± 0·76	ns	/
Iryanthera hostmannii						1·64 ± 0·16	ns	/
Iryanthera sagotiana			-0·64 ± 0·35			2·45 ± 0·22	ns	/
Jacaranda copaia	0·67 ± 0·27				-3·77 ± 2·49	3·80 ± 1·97	**	0·22
Lecythis persistens	0·19 ± 0·07	0·05 ± 0·48		-0·19 ± 0·11		0·98 ± 0·32	***	0·03
Lecythis poiteaui	0·29 ± 0·14	1·49 ± 0·83		-0·32 ± 0·17		-0·11 ± 0·63	*	0·11
Licania alba	0·06 ± 0·06	2·74 ± 1·40	-3·08 ± 0·97	0·16 ± 0·10		1·03 ± 0·48	***	0·11
Licania canescens		-5·80 ± 2·36	3·31 ± 1·67			3·76 ± 0·79	**	0·07
Licania densiflora						2·85 ± 0·16	ns	/
Licania heteromorpha	0·13 ± 0·07	14·49 ± 3·79	-9·16 ± 2·97			-1·74 ± 1·17	***	0·13
Licania membranacea	0·30 ± 0·10		-1·70 ± 0·91			3·33 ± 0·63	**	0·09
Licania ovalifolia						2·17 ± 0·19	ns	/
Licania sprucei	-0·86 ± 0·28	-21·60 ± 8·40	12·79 ± 7·04	1·46 ± 0·48		9·30 ± 2·57	***	0·41
Manilkara bidentata	0·45 ± 0·16					1·81 ± 0·59	**	0·29
Moronobea coccinea	-0·31 ± 0·37	-5·36 ± 2·78		1·15 ± 0·69		5·66 ± 1·49	*	0·10
Mouriri crassifolia	0·22 ± 0·09					1·76 ± 0·38	*	0·16
Oxandra asbeckii	0·08 ± 0·02	-8·59 ± 1·28	4·23 ± 0·59		-0·23 ± 0·14	5·34 ± 0·68	***	0·12
Pogonophora schomburgkiana	0·12 ± 0·03					1·31 ± 0·15	***	0·05
Poraqueiba guianensis	0·81 ± 0·34	7·22 ± 2·81		-1·23 ± 0·62		-2·52 ± 1·49	**	0·17
Pradosia cochlearia	0·65 ± 0·21	6·49 ± 2·94		-1·61 ± 0·63		0·26 ± 1·06	*	0·05
Qualea rosea		15·68 ± 6·54	-13·11 ± 6·71		-2·26 ± 0·98	2·46 ± 1·55	***	0·15
Recordoxylon speciosum		-2·27 ± 1·19			-1·28 ± 0·85	4·98 ± 0·75	*	0·06
Sextonia rubra		28·00 ± 11·31	-28·46 ± 12·72			-1·10 ± 2·03	*	0·15
Simaba cedron						0·65 ± 0·06	ns	/
Theobroma subincanum	0·30 ± 0·13					0·79 ± 0·52	***	0·22
Virola michelii	-0·89 ± 0·49	10·20 ± 10·36	-15·16 ± 7·32	2·04 ± 0·82		4·77 ± 3·48	**	0·20
Vouacapoua americana					-1·55 ± 0·99	2·79 ± 0·65	ns	/

Regression coefficients (μ: disturbance effect, λ: ontogenic linear effect, γ: ontogenic hump-shaped effect, ρ: disturbance × ontogeny effect, θ: competition effect, ω: intercepts (ω), coefficients of determination and P of complete models are reported. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; ns, not significant.
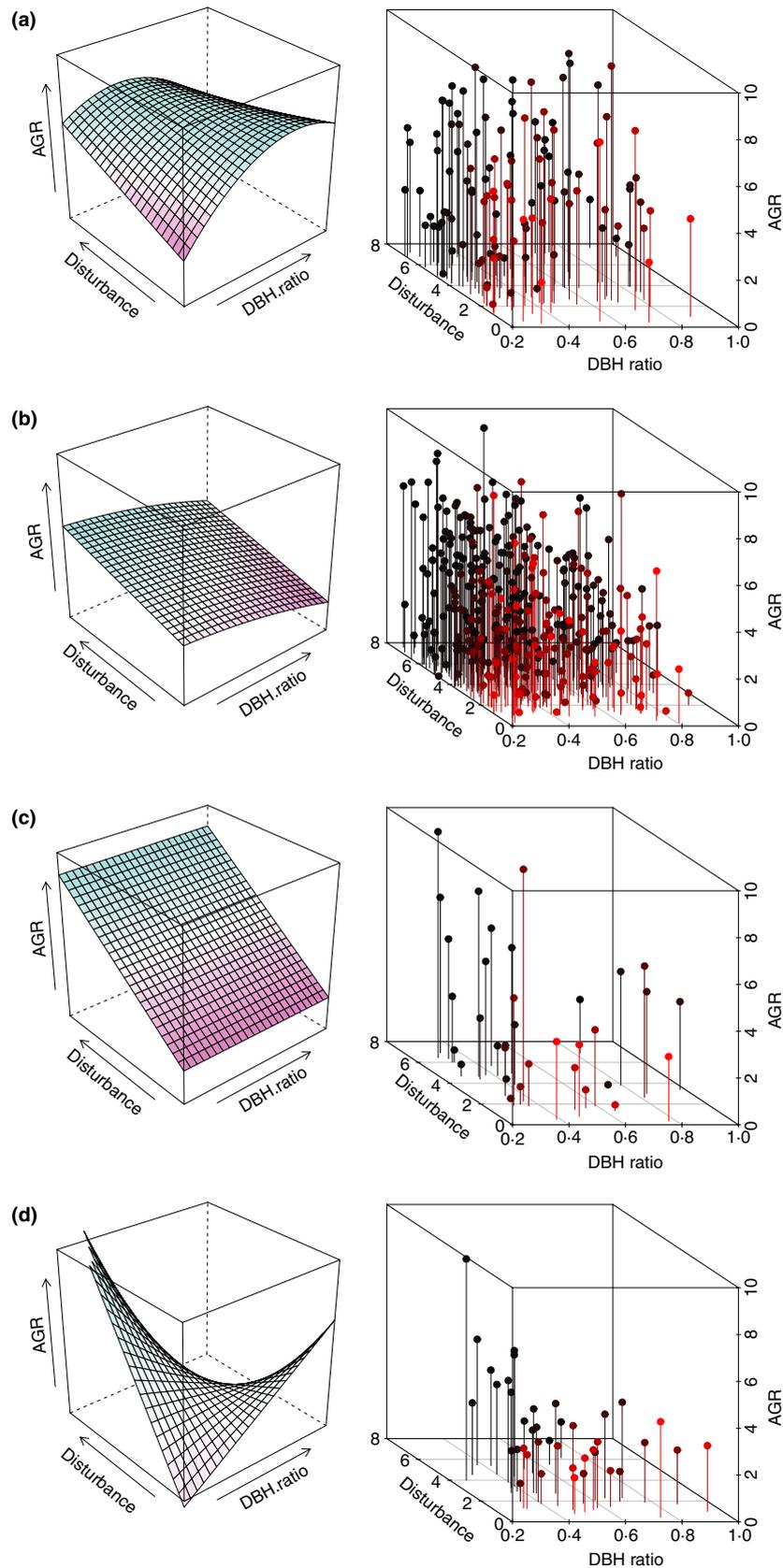
Fig. 2. Four representative growth models (a: *Dicorynia guianensis*, b: *Eperua falcata*, c: *Jacaranda copaia*, d: *Eschweilera decolorans*) across a realistic range of diameter at breast height ratio (*X* axis, 0·1–1·0) and disturbance index (*Y* axis, 0–8). Modelled annual growth rates (*Z* axis, 0·0–10·0) are estimated in mm year^{-1}. Observed growth data are provided in front of each corresponding growth model.
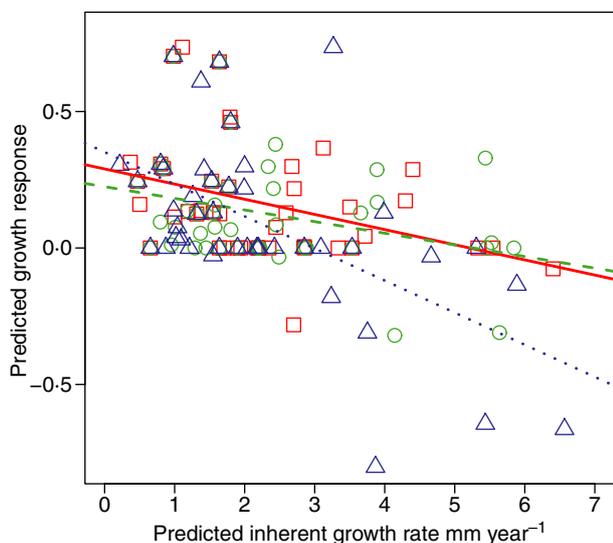
Fig. 3. Relationship between predicted inherent growth rate and predicted growth response to logging gaps at three ontogenetic stages (juvenile: red squares and solid line; young adult: green circles and dashed line; adult: blue triangle and dotted line) for 43 neotropical trees. Shown are parameter values for each species at each stage (points) and predictions from the analysis of covariance (lines). All slopes were significantly negative ($P \le 0.01$) and the adult stage was significantly different.

ontogeny, the stronger relationships (high λ, see Table 1) are found among canopy trees such as *Pradosia cochlearia*. As already shown by Clark & Clark (1999) for six Costa Rican canopy/emergent species, the inherent growth rate of these species did not decline toward zero as trees approached their maximum DBH. This means that these trees pursue an active growth until their death. This behaviour contrasts with the hump-backed pattern retained for eight species among which are also found numerous canopy/emergent species such as *Dicorynia guianensis* (Fig. 2a) that exhibit a gentle skew to the right. The low proportion of species showing a typical hump-backed pattern is consistent with results of Uriarte *et al.* (2004a). Together, these findings contradict the often-assumed hump-shaped curves and suggest that tropical tree growth curves display more complex behaviours.

Maximum DBH and seed mass were significantly strong predictors of species inherent growth. Maximum DBH was highly positively correlated with maximum height ($R^2 = 0.72$, $P \le 0.001$) among our 43 species and replacing DBH by height in the final model led to a very low increase in AIC (results not shown). We believe that this positive link between inherent growth rate and maximum DBH suggests that canopy/emergent species realize faster growth rates simply because they intercept more light due to their position in the forest canopy and because they have more potential for wood expansion in the bole. Studies from Malaysian (King, Davies & Noor 2006) and other neotropical rainforests (Poorter *et al.* 2008) also indicate that maximum size plays a fundamental role in tree growth rates (Vanclay 1991; Gourlet-Fleury & Houllier 2000). The observed decline in inherent growth rates with increasing seed mass is consistent with an adaptive syndrome in which

Table 2. Predicting inherent growth rates and growth responses to logging gaps using functional traits for 43 neotropical trees at three ontogenic stages

Ontogenic stage	Species inherent growth rate (predicted intercepts)						Species reaction to canopy gaps (predicted slopes)					
	Juvenile		Young adult		Adult		Juvenile		Young adult		Adult	
	E	F	E	F	E	F	E	F	E	F	E	F
Maximum DBH	0.036 ± 0.009	13.32	0.043 ± 0.009	19.23	0.038 ± 0.010	12.85	−0.005 ± 0.002	1.18	−0.006 ± 0.003	2.37	−0.006 ± 0.004	1.39
Seed mass	−0.032 ± 0.022	2.07	−0.038 ± 0.022	2.80	−0.050 ± 0.024	4.08	0.008 ± 0.004	2.28	0.011 ± 0.003	10.25	0.011 ± 0.005	3.91
Maximum height							0.013 ± 0.006	1.79	0.014 ± 0.005	0.65	0.013 ± 0.009	0.09
Stem architecture							0.184 ± 0.081	12.96				
Seedling ERS							−0.200 ± 0.112	3.19	−0.178 ± 0.104	2.61		
Seedling H							−0.176 ± 0.073		−0.148 ± 0.070			
Wood density									−0.355 ± 0.179	5.54	−0.585 ± 0.297	3.52
Intercept	0.681 ± 0.512		0.417 ± 0.515		0.597 ± 0.559		0.014 ± 0.133		0.264 ± 0.173		0.322 ± 0.268	
R^2_{model}	0.278		0.355		0.297		0.419		0.414		0.190	
P_{model}	<0.001		<0.001		<0.001		0.003		0.004		0.084	

The Akaike Information Criterion was used to choose the most parsimonious general linear model for each case. Model estimates (*E*), variance analyses *F* values (*F*), intercepts, coefficients of determination and *P* of final models are reported.
ERS, epigeal with reserve cotyledons; H, hypogeal; the reference group is epigeal with foliaceous cotyledons.

shade-tolerant species have large seeds to establish successfully but low inherent growth rates (Bloor & Grubb 2003; Baraloto, Forget & Goldberg 2005). However, contrary to our expectations and to the results from other recent studies (Poorter *et al.* 2008), wood density, which varied widely across Amazonian trees (Baker *et al.* 2004), was not a good predictor of the great inter-specific variation in inherent growth rates. High wood density has been suggested to contribute to lower growth rate because less volume is produced per unit biomass (King *et al.* 2005), but this is not supported by our results. For instance, the canopy tree *Eschweilera coriacea* (Lecythidaceae), which has a wood density of 0.84 g cm^{-3}, has one of the highest inherent growth rates observed (between 3.7 and 6.5 mm yeasr^{-1} depending on developmental stage), whereas the inherent growth of the light-wooded *Couratari multiflora* (also Lecythidaceae; density = 0.45 g cm^{-3}) was very low (0.9 mm year^{-1}).

GROWTH RESPONSES TO LOGGING GAPS

Distance to, rather than area of, logging gaps was the primary driver of the disturbance index (see Fig. 1). However, the optimum α was very low, suggesting that the distance of gap influence through light penetration in forest is relatively small. Generally, it is expected that the increasing irradiance within subcanopy layers that results from logging gaps will boost tree growth (positive μ), given that light is probably the most limiting factor affecting tree growth in tropical rainforests (Chazdon & Fetcher 1984; Denslow 1987; Bloor & Grubb 2003; King *et al.* 2005; Poorter *et al.* 2005). Indeed, the disturbance index was retained in 30 of 43 specific growth models and negative μ occurred only in three species. And these three negative μ were always corrected by a positive ρ for large DBH. This means that even if young trees were negatively affected by gaps, adult trees were not. A possible explanation might be that young trees from these three species, when grown at full irradiance, have suffered from water limitations that lead trees to compensate for increasing transpiration losses by allocating a larger biomass to their root system (Poorter 1999).

Specific growth responses to logging gaps are closely related to six out of the seven studied functional traits. The retention of maximum DBH and Seed mass in the final models may be related to the negative relationship between inherent growth rate and growth response to disturbance (Fig. 3), which results in traits that are positively correlated with species inherent growth rates to be negative predictors of species growth response and vice versa. Maximum tree height was correlated with species reaction at the juvenile stages. As juveniles from taller species may intercept a greater amount of incident light when compared with juveniles from smaller species at a similar DBH ratio, taller species may have greater reaction to logging gaps. These trees may also respond more to logging gaps simply because they are more demanding of light, given that these species are canopy/emergent trees (Poorter *et al.* 2005). With some exceptions, these light-demanding species also have an orthotropic growth and a less-dense wood (Table 2) that

ensures an efficient and costless growth response to increasing light incidences when compared with plagiotropic heavy-woody trees (Poorter, Bongers & Bongers 2006). Finally, seedling morphologies are an important component of plant regeneration strategies, strongly affecting seedling growth such that seedlings with foliar cotyledons generally grow faster than seedlings with reserve-type cotyledons (Baraloto & Forget 2007). Our study has extended this finding to the adult tree stage. Tree species with foliaceous cotyledons also respond better to canopy opening than do species with reserve-type cotyledons (Table 2).

Although it has been postulated that tree growth response to increasing light availability changes with ontogeny (Baraloto, Goldberg & Bonal 2005), few data exist to test this hypothesis for a large number of species. Our results revealed two contrasting ecological behaviours. First, the growth rates of four species decreased with increasing gap proximity when young and increased when old. In other words, young trees performed better in shaded unlogged environments while old trees grew faster with increasing light. This strategy can be linked to a null model of light vertical distribution (Poorter *et al.* 2005), meaning that optimum inherent growth in forests naturally follows incident light levels through vertical strata. Alternatively, these older larger trees may have developed deep tap roots that maintain high levels of growth by absorbing water from the deep soils during the dry periods (Nepstad *et al.* 1994). However, our data suggest that this strategy was not the most common. Indeed, 8 of 43 species had young individuals growing faster near gaps whereas older trees grew faster further from gaps (Fig. 2a). This behaviour appears to represent two distinct ecological groups. First, understorey and subcanopy species (e.g. *Bocoa prouacensis*) perform better in near-gap high-light environments when young probably because they adjust their light-growth performance with age when they are most frequently overtopped by canopy and emergent trees. The second group includes canopy/emergent trees (*Pradosia cochlearia*, *Dicorynia guianensis*) that may not change optimum light environments with age but rather overtops all other trees when larger and thus do not depend on logging gaps for growth. That these trees perform better, when old, far from logging gaps may be link to a greater sensitivity to environmental changes in logging gaps. For example, it has been suggested that logging gaps dry out and have lower humidity due to the direct sunlight (Olander *et al.* 2005), although we did not measure these environmental factors in our study.

Our results highlight an unexpected tradeoff between inherent growth rate and growth response to logging gaps (Fig. 3). A potential bias in this result could be that light-demanding species were only sampled near logging gaps. However, our result is particularly noteworthy because (i) the stems of light-demanding species in our sample (>10 cm DBH) were all present before logging gaps were created and (ii) inherent growth rates were all predicted for a standardized competition index, i.e. in a similar forest environment before logging. These observations suggest that crop trees of slower-growing commercial species will grow larger near logging gaps relative

to more rapidly growing species for which logging gaps may favour seedling recruitment more than adult growth (Nussbaum, Anderson & Spencer 1995).

SYNTHESIS AND APPLICATIONS

Tropical forests are usually harvested by selective logging (Putz *et al.* 2008) but it is rarely an isolated activity and frequently leads to other disturbances (Asner *et al.* 2006). Often, the skid trail and road system used to remove timber from forest sites is subsequently used by colonists who hunt, remove more timber, or clear land for agriculture. At Paracou, the research site was protected against these threats and similar protection will probably be necessary in other tropical forests, either by local landholders and/or regional managers, to enable selectively logged forests to recover carbon lost to emissions (Blanc *et al.* 2009). Nonetheless, our results have clear management implications:

1. Distance to, rather than area of, logging gaps was found to be the primary driver of the disturbance index suggesting that, for the same logging intensity, numerous single-tree logging gaps should be favoured over fewer multiple-tree gaps in order to increase the growth of the remnant trees. In other words, the time to recover timber volume and aboveground biomass removed by logging will be shorter if several small-scale logging operations are carried out in preference to a single large-scale forestry operation.

2. The trade-off between growth responses and inherent growth rate clearly showed that species having low inherent growth rates grew faster when close to logging gaps. This is interesting because most timber tree species have low inherent growth rates in the neotropics (Guitet *et al.* 2009). Therefore, in terms of tree growth (recruitment and/or mortality rates may respond differently), these timber species are the most favoured by logging.

3. Growth rates and growth responses varied substantially with tree size, suggesting that species-specific harvest prescriptions may be necessary to ensure that future crop trees take the advantage of light availability arising from logging gaps. Forest-logging operations should be conducted very carefully to respect pre-logging harvest prescriptions.

Improved information about the spatial typology of logging gaps will be more readily obtained in the near future from physical measures such as laser profilers (LIDAR) and very high spatial resolution optic/radar imagery (Palace *et al.* 2008). With such data, our method will allow post-logging tree growth in tropical forests to be modelled and it is sufficiently general to apply to a broad range of tropical forests. The method disentangles the effects of logging and individual size on tree growth and it provides robust estimates for the value of inherent growth rate and tree response to logging for individual species. This is a necessary step towards describing the diversity of adult tree growth responses to logging gaps, but much work is needed before we can effectively parameterize species growth functions when modelling forest response to logging practices. Although few comparative data sets are available from tropical forests, many forestry experiments have been conducted at other sites (e.g. Vanclay 1991; Sheil, Jennings & Savill 2000). With relatively little extra work (resolving botanical determinations and describing functional traits), our approach can be applied to more tropical trees and sites (Peacock *et al.* 2007) allowing us to model the post-logging dynamics of these complex ecological systems (Clark & Clark 1999).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. A summary of the functional traits of the 43 species studied, including position in forest layers (1: understorey, 2: dominated in canopy, 3: dominating in canopy, 4: emergent), stem architecture (0: plagiotropic, 1: orthotropic), tree height in m, wood density at 12% moisture in g cm^{-3}, maximum DBH in cm, seedling

morphology (1: epigeal with foliaceous cotyledon, 2: epigeal with reserve storage, 3: hypogeal), mass of seeds in g.

Appendix S2. Graphical displays of the 34 significant growth models across a standardized range of DBH ratio (X axis, 0·2–1·0), disturbance index (Y axis, 0–8) and modelled annual growth rates (Z axis, 0·0–10·0, estimated in mm year^{-1}).

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