

IMPACTS OF LOGGING IN TROPICAL RAIN FORESTS WITH DISTURBED RECRUITMENT - A SIMULATION STUDY

Andreas Huth^{1*}, Peter Köhler²

¹Center for Environmental Research Leipzig-Halle
Department of Ecological Modelling
P.O. Box 500 136, D-04301 Leipzig, Germany
huth@oesa.ufz.de

²Alfred Wegener Institute for Polar and Marine Research
PO Box 12 01 61, D-27515 Bremerhaven, Germany
pkoeehler@awi-bremerhaven.de

Keywords: forest growth model, logging impacts, process-based model, recruitment, tropical rain forest

Summary. *There are increasing evidences that recruitment of trees might be endangered through events such as climate change, enhanced seed predation or fragmentation. In addition, continuing logging in the tropics is making the conservation of remaining forests increasingly difficult. In this study we assess various impacts of recruitment shortage and tree harvesting in a tropical rain forest in Sabah, Malaysia. 56 different scenarios using the process-based forest growth model Formind2.0 were assessed. Formind2.0 is based on the calculations of the carbon balance of individual trees belonging to 13 different plant functional types.*

Reduced recruitment led to shifts in the abundances of species, to species loss, and to forest decline and dieback.. Reduced-impact logging methods were compared with conventional logging methods.

1. Introduction

There are evidences that tree recruitment in the tropics might be short in the future. Up to 80 % of the dominant trees in South-East Asia belong to the dipterocarp tree family. Their recruitment mechanisms prevail seed predation through mass flowering followed by mast fruiting events on a 2-10 yrs basis. The mass flowering strongly depends on the El Niño Southern Oscillation (Curran et al. 1999). The proposed climate change might also change the time and frequency of the necessary low night-time temperatures which trigger this mass flowering (Yasuda et al. 1999). Additionally, forest fragmentation might extinct key species important for seed dispersal and thus alter fauna-flora interactions (da Silva and Tabarelli 2000). Human pressure in form of land-use change or tree logging might led to a migration of huge populations of seed predators and thus the number of ingrowing seedlings might be reduced several orders of magnitude (Curran et al. 1999). However, present knowledge on recruitment and recruitment rates in tropical forests is still limited because recruitment is subject to many factors (Clark et al. 1999, Duncan and Chapman 1999, Webb and Peart 1999).

In recent reviews (Bugmann et al. 2001) the limitations and shortcomings of the applications of forest models to climate change analysis were highlighted. Within these studies the impacts on the complex regeneration processes (including seed production, dispersal, and germination) were discussed (Price et al. 2001). It was stated that detailed descriptions of the different processes of the recruitment is essential. Since the climate change impacts on various ecophysiological processes - especially in the tropics - are

*Both authors contributed to this paper equally. The presented study is part of the Ph. D. Thesis of P. Köhler.

not fully understood so far we think, one first approach is a simulation analysis evaluating the importance of regeneration on the forest dynamics.

Furthermore, the impacts of tree harvesting on tropical forest structure and growth are widely discussed topics (Pinard and Putz 1996, Whitmore 1998). The damage to the residual forest varies considerably for different logging techniques and cycles. A forest logged using methods of reduced-impact logging is expected to decrease damages and increase economic profit compared to a conventionally logged forest (Barreto et al. 1998). Criteria for sustainable forest management and the ecological certification of timber are the subject of much current debate (Rice et al. 1997, Bowles et al. 1998).

Computerised simulation models designed to estimate the growth and yield of tropical rain forest are a useful tool to broaden the current discussion (Boott-Gullison 1995, Clark and Clark 1999). In combining the two aspects recruitment shortage and tree harvesting in a simulation study for a forest reserve in Sabah, Malaysia, we try to analyse future threats of tropical rain forests.

The simulation model used in this study is the process-based forest growth model FORMIND2.0. FORMIND (Koehler and Huth 1998) was developed following an individual-oriented approach. It was used to evaluate the approach of the more aggregated model FORMIX3 (Huth and Ditzer 2000, 2001, Kammesheidt et al. 2002, Glauner et al. 2003). One important feature of both models is the grouping of species into plant functional types PFT (Koehler et al. 2000). A careful comparison of measured and simulated growth with FORMIND for different forest stands in Sabah, Malaysia was used to validate the growth and competition processes included in the model (Koehler et al. 2001). The model was recently used to simulate growth and yield in the rain forests of Venezuela and French Guyana (Kammesheidt et al. 2001, Köhler et al. 2003).

In this study we want to answer the following questions for a tropical forest stand in Sabah, Malaysia, and discuss the relevance of our findings for other regions. (1) How does a shortage in recruitment influence structural and compositional forest dynamics? (2) How do harvesting practises and rotation length influence the dynamics in forests threatened by recruitment shortage?

2. Methods

2.1 Area description

We simulate growth and logging of the tropical rain forest of the Deramakot Forest Reserve (DFR) situated in Sabah (North Borneo, Malaysia, 117°30' E, 5°5' N, 130–300 m asl.). Deramakot has a per-humid climate with a mean annual temperature of 27 °C with little seasonal variations. The average annual precipitation is about 3500 mm, with no pronounced dry season. The soils are low in nutrients and prone to erosion once left devoid of tree cover. The dominant prevailing forest type is lowland Dipterocarp forest (Schlensog 1997). Commercial logging started in the 1950s with varying intensity and damages. The average annual precipitation is about 3500 mm, with no pronounced dry season.

2.1 Species grouping

The shrub and tree species (total number: 468 species) were assigned to 13 different plant functional types (PFT) based on their successional status and maximum height at maturity.

The successional status (early, mid, or late) was determined by their growth rates under various light regimes, as well as through a survey of wood densities, which are good indicators of growth rates for most species. A species list including grouping is available online (<http://www.usf.uni-kassel.de/usf/archiv/dokumente.en.htm>). A detailed description and validation of the grouping concept and its application to Sabah was published elsewhere (Koehler et al. 2000). Similar grouping concepts are found in Manokaran Swaine 1994, Thomas Bazzaz 1999.

In addition, subgrouping into commercial and non-commercial species is performed for all mid- and late successional species. Since detailed information of the commercial status was not available at the species level, 80% of mid- and late successional species are considered commercial timber. In the analysis and

for the sake of simplicity, we only distinguish our results between the three different successional status (early, mid, and late).

2.2. Description of the model

FORMIND2.0 is an individual-oriented process-based forest growth model for the simulation of the spatial and temporal development of unevenly-aged mixed forest stands (Koehler and Huth 1998, Koehler et al. 2001). A complete description including all the relevant functional relationships of the model version FORMIND2.0 was published elsewhere (Kammesheidt et al. 2001). After a short general description, we concentrate in the following on the recruitment module.

The model describes forest dynamics as a mosaic of interacting forest patches measuring 20 m x 20 m. Within these patches trees are not spatially explicitly distributed, and thus all compete for light and space following the gap model approach (Shugart 1998). Allometric relationships connect the above-ground biomass of a tree with its stem diameter, the tree height, the bole volume and the crown dimensions. Using these relationships, the distribution of individual tree crowns and their leaf area in the canopy is calculated in horizontal canopy layers with a width of 0.5 m. The growth of an individual tree is based on a carbon balance. Calculations include the photoproduction of the trees and assimilate losses due to respiration, litter-fall and fine root decay. Within a patch, vertical light attenuation in the canopy is calculated from light intensity above the canopy with respect to the absorption of tree crowns. The dependence of specific photosynthetic productivity on irradiance is modelled using a Michaelis-Menten-type light response curve. Photoproduction P is calculated from the tree's leaf area. We assume an increasing limitation effect of water transport deficiencies with increasing tree height (Ryan et al. 1997). Thus, actual productivity is calculated by applying a size-dependent limitation factor q . Assimilation losses are estimated in relation to tree biomass. We distinguish between biomass-dependent maintenance respiration R_M and growth respiration R_G . Our main time-dependent growth equation for the biomass B_i of one tree is

$$\frac{dB_i}{dt} = P \cdot q \cdot (1 - R_G) - R_M \quad (1)$$

Tree growth is calculated in annual time steps. Competition is modelled in terms of competition for light and space, the latter resulting in self-thinning. For small trees (diameter < 10 cm) a diameter-dependent mortality is added to a basic mortality rate. Trees resulting in crown closure are eliminated to avoid crowding (self-thinning). Mortality is modelled as a stochastic event. Senescent trees die and collapse with a certain probability, knocking down smaller trees in neighbouring patches and creating gaps of a size depending upon their crown size.

Two different recruitment mechanisms were incorporated in the model. The simplest approach (called CONSTANT) assumes that an intact forest has a constant seed input rate, which is a well-supported approach for undisturbed forests. The second approach (called LOCAL) takes into account the dispersal of seeds produced from local mother trees, i.e. trees exceeding a certain size. This second approach is necessary for assumptions on recruitment shortages. As recruitment strategies are highly variable in rain forests, with interspecific differences in fruiting period, number of seeds, seed sizes, dispersal strategies, agents, and distances, seed survival, germination probabilities and maturing size of seed disperser (review in Clark et al. 1999, Harms et al. 2000). Although different dispersal agents (e.g. wind, birds, mammals) are not directly distinguished in our model, the resulting average dispersal distance d depends upon the species and they should match with the parameter set. From the dispersal kernels discussed by Clark et al. 1999 we use the approach based on a Gaussian distribution. Thus, 99 % of the seeds are dispersed at a distance less than $2.12 d$.

The actual dispersal distance is randomly drawn from the probability distribution, and the dispersal direction is drawn uniformly. The resulting seed shadow is the product of the rate of seed production and the dispersal kernel. For both recruitment mechanisms, incoming seeds update a seed pool, taking into account the dormancy variability across functional groups. These seeds correspond to the reproductive success and are those which can potentially be established at the minimum diameter of 1 cm. Seed loss

due to predators is implicitly included in relatively low seed production rates. Actual seed germination depends upon understorey light intensities.

2.2 Parameters and Initialisation

The parameter set used in our simulations is documented in Köhler (2000). The seed production rates per mother tree (LOCAL recruitment) and the constant seed input rates (CONSTANT recruitment) were estimated from a sensitivity analysis of long-term runs of the primary stand P1, assuming a dynamic equilibrium of the primary forest structure and its species composition. They fit seedling numbers found in our inventories (Schlensog 1997). If seed predation was not implicitly included in our seed production rate and was estimated from current measurements (Curran and Webb 2000) the number of seeds in the seed pool ranged between 100,000 and 200,000 per ha, which corresponded well to observations (Curran and Webb 2000). In both stands (P1, L1), trees were distributed randomly among the 5x5=25 patches of one hectare. P1 contained almost no early successional species, abundance being highest in the large growing mid- (PFT 12: 37%) and late successional species (PFT 13: 20%). The site L1 was dominated by medium-sized early successional species (PFT 5: 66%), and contained nearly no late successional species. The seed pool was filled with average seed numbers from long-term simulations.

2.3 Simulation scenarios

We designed 56 different simulation scenarios for this study. The scenarios differ in at least one factor: recruitment shortage, logging method, or length of logging cycle. The area size was kept constant at 9 ha; we assumed the boundary conditions to be periodic.

Recruitment shortage. - In former studies using FORMIND, recruitment was modelled on the basis of the constant input of seeds over the whole simulation area (corresponding to the CONSTANT recruitment approach). As recruitment might be threatened by various factors these assumption might be too simplistic for the future. The explicit seed dispersal was modelled in the alternative approach called LOCAL, which is necessary for our studies. Even if the impacts which threaten tree recruitment influence different aspects of the recruitment process -- climate change alters fruiting frequency (Yasuda et al. 1999), extinct fauna species alter seed dispersal and germination (da Silva and Tabarelli 2000), increasing numbers of seed predators increase the seed mortality (Curran et al. 1999) -- in our simulation scenarios we only change the seed production rates. Seven scenarios with different reduction of recruitment rates were defined from a forest with constant seed production (reference case) to a forest without any recruitment at all (labelled *rec000*). The last scenario might be very unlikely but it gives us the possibility to analyse the underlying model dynamics independent on the recruitment module. The numbers of dispersed seeds per mother tree and the constant seedling input were modified from standard values

Logging (methods and cycle length). - Our modelling of logging practices was motivated by several studies (Ditzer et al. 2000, Kammesheidt et al. 2001). Two methods were distinguished: highly damaging conventional logging (CON), which generally makes use of heavy machinery, unskilled workers and little planning effort, and reduced-impact logging (RIL), where substantial planning for road construction, felling directions etc. is performed. In RIL, tree removal usually implies the use of winching cables or air-borne cable systems.

The differences modelled between the two methods were the logging impact on the residual stand. We distinguished (1) damage through tree felling, (2) skidding damage in the patch of a felled tree, (3) area loss due to road construction and log landings, and (4) increased mortality rates for ten years after logging. The tree-fell damage was proportional to crown size and method-independent. The felling direction was chosen randomly in CON, but directed towards neighbouring gaps in RIL whenever possible. In the patches where felled trees were situated, 25% and 55% of the stems were killed through skidding in RIL and CON, respectively. Area loss was simulated by the complete removal of the residual stand in 12% (RIL) and 33% (CON) of randomly chosen patches. The mortality in the years after logging was twice (RIL) and three times (CON) higher than normal accounting for damaged but not instantly destroyed trees.

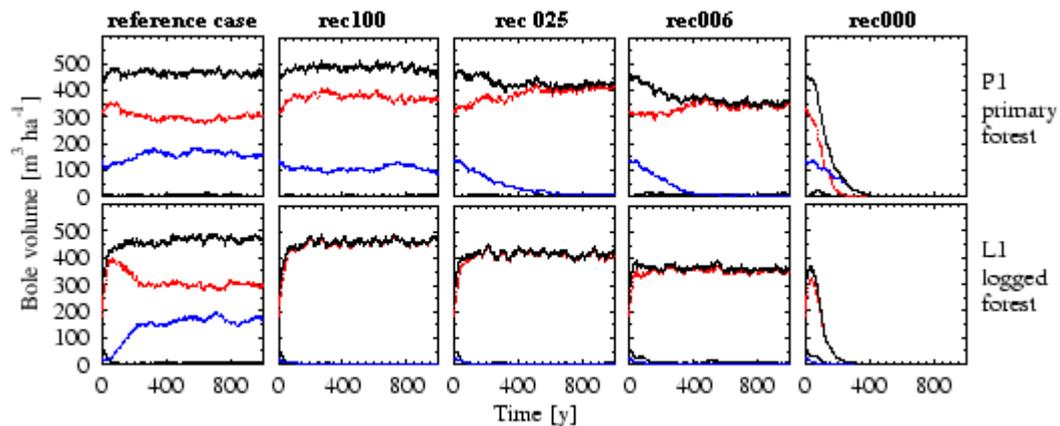


Figure 1 Selected time series of bole volume (m^3/ha) for primary and logged forest with different recruitment shortage (*reference case*, *rec100*, *rec025*, *rec006* and *rec000*).. Simulation of 1000 y of an area of 25 ha. Total (solid bold line), early successional spp. (solid line), mid-successional spp. (broken dotted line), late successional spp. (broken line).

The time between two harvesting operations was varied in steps of 20 y between 20 y and 80 y. The stand L1 was recorded directly after a logging operation; therefore the first logging starts right after one cycle length. All commercial trees of the mid- and late successional species with a minimum diameter of 60 cm were removed in a logging operation.

3. Results

Influence of recruitment shortage on undisturbed forest dynamics

Fig. 1 shows forest dynamics under recruitment shortage without logging. In the reference scenario (normal recruitment) the primary (P1) and the logged (L1) forests have the same average total bole volume (457-465 m^3/ha) and the same species composition in the long term (early/mid-/late successional species: P1: 1/68/31%, L1: 1/65/34%). However, with recruitment shortage species composition is strongly modified. Simulations of primary and logged forest stand led both to an extinction of the late successional species, in logged forests this extinction will happen much faster (in the next hundred years). The logged forest shows in the scenario with full local recruitment (*rec100*) already this strongly modified dynamics (in contrary to the primary forest). This demonstrates that the logging history of a forest may influence its future species composition severely.

In scenario *rec006*, the total bole volume was reduced to 350 m^3/ha for both P1 and L1. The total bole volume and species composition varied significantly as a result of the shortage in recruitment (ANOVA: $P < 0.001$, $P < 0.05$, respectively). In the dramatic event of the total loss of the seed supply (scenario *rec000*), possibly through enhanced seed predation coupled with low seed production due to El Niño events (Curran and Leighton 2000), the recruitment shortage led to a collapse of the forest structure, albeit only after about 300 and 200 y for primary (P1) and logged (L1) forest, respectively (Fig. 1). In the latter case the bole volume first increased from 280 m^3/ha to 400 m^3/ha before decreasing.

Influence of recruitment shortage on logged forests

Fig. 2 shows forest dynamics under recruitment shortage assuming two different logging methods (reduced-impact RIL, conventional CON) and logging cycles (20 and 80 years). The mean abundance of early successional species varied between 5% and 54%, and of late successional species between 1% and 14%. The changes of the abundance of early and late successional species with respect to logging cycles, methods, and recruitment shortage were significant ($P < 0.001$). The higher the recruitment shortage, the more was the species composition shifted towards early successional species (without scenario *rec000*).

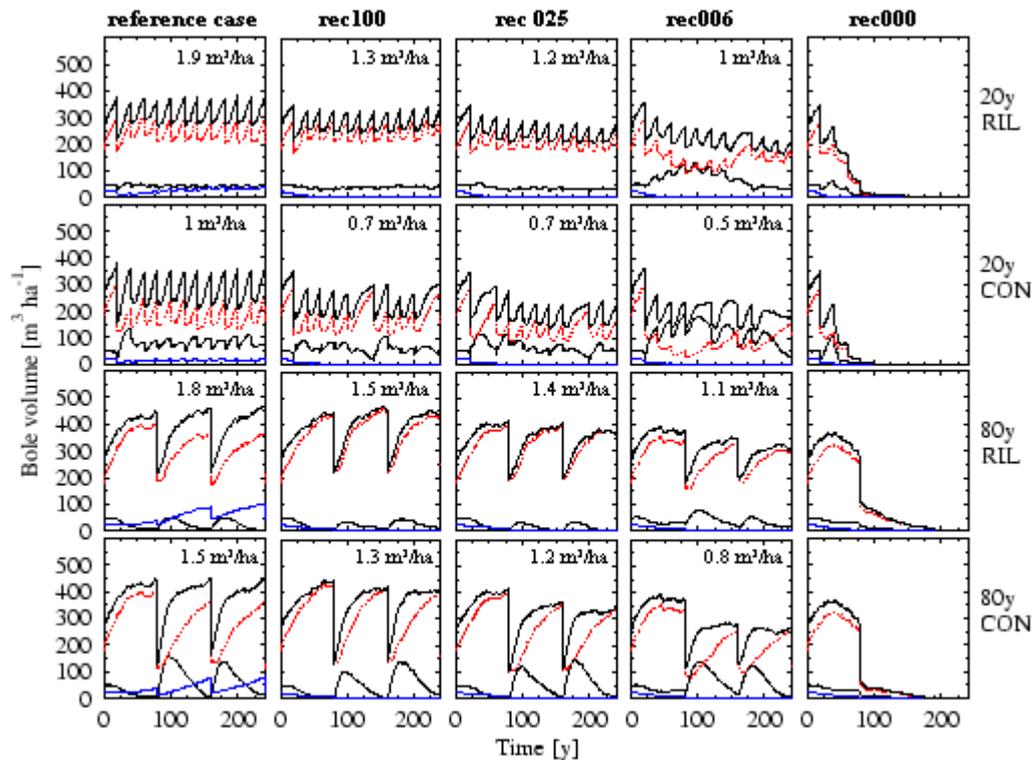


Figure 2 Selected time series of bole volume (m^3/ha) for different scenarios. Simulation of 9 ha over 240 y of logged forest at site L1. Variation of logging cycle (20 y; 80 y), method (RIL: reduced-impact; CON: conventional) and recruitment shortage (*reference case*, *rec100*, *rec025*, *rec006* and *rec000*). Total (solid bold line), early successional spp. (solid line), mid-successional spp. (broken dotted line), late successional spp. (broken line). Numbers in the graphics indicate the mean gross yields per year (in m^3 stem volume per ha).

Conventional logging favoured the abundance of early successional species and suppressed the development of late successional species. The abundance of early successional species increased drastically after events of conventional logging; short logging cycles gave the forest no time to recover the total standing bole volume. Furthermore, logging in forest with reduced recruitment resulted in a constant decline of total bole volume. Here, short logging cycles produced an increase in the number of suspended logging operations because of the lack of harvestable trees. The extinction of late successional species was detectable in all scenarios of reduced recruitment with conventional logging methods after 100 simulated years; by applying reduced-impact methods a very small fraction ($< 1\%$) survived. When conventional logging methods and short (≤ 40 years) cycles were applied in forests with highly limited recruitment, the stand was dominated by early successional species over several decades or even centuries. Any tree extraction in the scenario *rec000* accelerated forest decline rapidly.

Additional analysis shows that yields strongly decrease due to recruitment shortage (Fig. 2). We suppose in the simulations that successional species include the same fraction of commercials as for the late successional species. If we would assume a lower fraction yields would be much lower. The low impact logging scenarios have always higher yields than the corresponding conventional scenarios.

4. Discussion

In our simulations the total simulated bole volume was similar for the reference case and under low recruitment shortage, but declined in scenarios of higher recruitment shortage. Furthermore, it turned out that even in scenarios without any recruitment (*rec000*) the standing volume was only affected with a time-lag of about a half a century. Thus, the standing bole volume, the numbers of saplings or mother trees are not appropriate indicators for detecting early stages of forest dieback. The important variables for the identification of a forest decline are the recruitment and the mortality rates. Natural recruitment thus acts as a buffer system for stand development (Warner and Chesson 1985). Any changes in seed production rates are buffered over at least one order of magnitude. Species shift is a fast response of forests under recruitment shortage to single logging events. Furthermore, the simulations suggest a forest decline if the recruitment rates drop below 1/10 of their normal values. Our simulations predict strong species shifts in forests under strong recruitment pressure during the next centuries. Current field studies have already detected that regeneration rates in forest fragments are biased towards families of early successional species (Laurance et al. 1998, Benitez-Malvido 1998) or a reduction of the total recruitment in the core of forest fragments occurred (Bierregaard et al. 1992). The species loss of fauna populations in forest fragments has been the subject of several studies (review in Turner 1996). Up to now only a few empirical studies have detected changes in the species composition of the plant communities in fragmented forests (Turner et al. 1995, Tabarelli et al. 1999).

One key process in forests with recruitment shortage is seed dispersal. The complex interactions between fauna and flora need to be studied in more detail in the future. However, as one first step logging impacts on bird communities were assessed with a simulation study recently (Koehler et al. 2002). Thus, the feedback of the fauna via recruitment failure on the flora - which was proposed here without quantifying its reasons in detail - might be analysed further. For the rain forests in South-East Asia the mass flowering seems to be one of the key processes, thus the impacts of a temperature increase might effect the whole area. However, the floral trigger responsible for mass flowering seems to be driven by different events and is correlated with La Niña phases on the Malay Peninsula, but with El Niño phases in the eastern part of South-East Asia (Yasuda et al. 1999). On the other hand the extinction of key dispersal bird species might be of minor importance in this area, because the seeds of dipterocarp tree species are mostly wind dispersed. (Whitmore 1998)

Conclusions

Recruitment shortage - either induced through climate change, extinction of key dispersal species, or enhanced seed predation - will alter future species composition in tropical rain forests. This might especially be the case for forest sites in South-East Asia, whose recruitment depends strongly on mass flowering events.

Further impacts through tree harvesting might not only amplify this shift in tree species abundance, but might also lead to forest decline and dieback. Logging yields are expected to be reduced significantly in future times. Within this situation the use of reduced-impact logging methods together with long logging cycles provide the approach to reduce impacts on the forest ecosystem.

5. Acknowledgements

We thank specially T. Ditzer for his contributions. We thank H. Bossel, J. Chave, R. Glauner, L. Kammesheidt and K. Wirtz for their helpful comments. P. Köhler was funded by the Otto Braun Foundation of University of Kassel, Germany.

6. References

Barreto, P., Amaral, P., Vidal, E., and Uhl, C. (1998), "Costs and benefits of forest management for timber production in eastern Amazonia", *Forest Ecology and Management*, 108, 9-26.

Benitez-Malvido, J. (1998), "Impact of forest fragmentation on seedling abundance in a tropical rain forest," *Conservation Biology*, 12, 380-389.

- Bierregaard, R. O., Lovejoy, T. E., Kapos, V., dos Santos, A. A., and Hutchings, R. W. (1992), „The biological dynamics of tropical rainforest fragments,“ *BioScience*, 42, 859-866.
- Boot, R. G. A. and Gullison, R. E. (1995), “Approaches to developing sustainable extraction systems for tropical forest products,“ *Ecological Applications*, 5, 894-903.
- Bowles, I. A., Rice, R. E., Mittermeier, R. A., and da Fonseca, G. A. B. (1998), “Logging and tropical forest conservation,“ *Science*, 280, 1899-1900.
- Bugmann, H. K. M James F. Reynolds, Louis F. Pitelka. (2001), „How much physiology is needed in forest gap models for simulating long-term vegetation response to global change?“ *Climatic. Change*, 51, 249-250..
- Clark, D. A. and Clark, D. B. (1999), “Assessing the growth of tropical rain forest trees: Issues for forest modeling and management“, *Ecological Applications*, 3, 981-997.
- Clark, J. S., Silman, M., Kern, R., Macklin, E., and HilleRisLambers, J. (1999), “Seed dispersal near and far: pattern across temperate and tropical forests,“ *Ecology*, 80, 1475-1494.
- Curran, L. M., Caniago, I., Paoli, G. D., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C. E., and Haeruman, H. (1999), “Impact of El Niño and logging on canopy tree recruitment in Borneo,“ *Science*, 286, 2184-2188.
- Curran, L. M. and Leighton, M. (2000), “Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae,“ *Ecological Monographs*, 70, 101-128.
- Curran, L. M. and Webb, C. O. (2000), “Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae,“ *Ecological Monographs*, 70, 129-148.
- da Silva, J. M. C. and Tabarelli, M. (2000), “Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil,“ *Nature*, 404, 72-74.
- Ditzer, T., Glauner, R., Förster, M., Köhler, P., and Huth, A. (2000), “The process-based stand growth model FORMIX3-Q applied in a GIS-environment for growth and yield analysis in a tropical rain forest,“ *Tree Physiology*, 20, 367-381.
- Duncan, R. S. and Chapman, C. A. (1999), “Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa,“ *Ecological Applications*, 9, 998-1008.
- Glauner, R.; Ditzer, T.; Huth, A. (2003), “A new approach for AAC calculation in tropical moist forest. An example from Sabah, Malaysia,“ *Canadian Journal of Forest Research*, 33, 1-15.
- Harms, K. E., Wright, S. J., Calderon, O., Hernandez, A., and Herre, E. A. (2000), „Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest,“ *Nature*, 404, 493-495.
- Huth, A. and Ditzer, T. (2000), “Simulation of the growth of tropical rain forests - FORMIX3,“ *Ecological Modelling*, 134, 1-25.
- Huth, A. and Ditzer, T. (2001), “Long-term impacts of logging in a tropical rain forest - a simulation study,“ *Forest Ecology and Management*, 142, 33-51.
- Huth, A., Drechsler, M., Köhler, P. (2003), “Multicriteria analysis of logging scenarios in a tropical rain forest,“ *Canadian Journal of Forest Research*, submitted.
- Kammesheidt, L., Köhler, P., and Huth, A. (2001), “Sustainable timber harvesting in Venezuela: a modelling approach,“ *Journal of Applied Ecology*, 38, 756-770.

Kammesheidt, L., Köhler, P., and Huth, A. (2002), "Simulating logging scenarios in secondary forest embedded in a fragmented neotropical landscape," *Forest Ecology and Management* 170, 89-105.

Köhler, P. (2000), *Modelling anthropogenic impacts on the growth of tropical rain forests - using an individual-oriented forest growth model for analyses of logging and fragmentation in three case studies*. PhD thesis, University of Kassel. Der Andere Verlag: Osnabrück .

Köhler, P., Ditzer, T., and Huth, A. (2000), „Concepts for the aggregation of tropical tree species into functional types and the application on Sabah“s lowland rain forests,“ *Journal of Tropical Ecology* 16, 591-602.

Köhler, P., Ditzer, T., Ong, R. C., and Huth, A. (2001), „Comparison of measured and modelled growth on permanent plots in Sabahs rain forests,“ *Forest Ecology and Management* 144, 101-111.

Köhler, P. and Huth, A. (1998), „The effect of tree species grouping in tropical rain forest modelling - Simulation with the individual based model FORMIND,“ *Ecological Modelling* 109, 301-321.

.Köhler, P.;Reinhard, K.; Huth, A. (2002), "Simulating anthropogenic impacts to bird communities in tropical rain forest," *Biological Conservation*, 8, 35-47

Köhler, P., Chave, J., Riera, B., Huth, A. (2003), "Simulating long-term response of tropical wet forests to fragmentation," *Ecosystems* 2, in press.

Laurance, W. F., Ferreira, L. V., Rankin-deMerona, J. M., and Laurance, S. G. (1998), „Rain forest fragmentation and the dynamics of Amazonian tree communities,“ *Ecology* 79, 2032-2040.

Manokaran, N. and Swaine, M. D. (1994), "Population Dynamics of Trees in Dipterocarp Forests of Peninsular Malaysia, No. 40" in *Malaysian Forest Records*, Forest Research Institute of Malaysia, Kuala Lumpur .

Pinard, M. A. and Putz, F. E. (1996), „Retaining forest biomass by reducing logging damage,“ *Biotropica* 28, 278-295.

Price,D.T.,Zimmerman,N.E.,vanderMeer,P.J.,Lexer,M.J.,Leadley,P.,Jorritsma,I.T.M., Schaber, J., Clark, D. F., Lasch, P., McNulty, S., Wu, J., and Smith, B. (2001), „Regeneration in. Gap Models: Priority Issues for Studying Forest Responses to Climate Change“, *Climatic Change*51, 475-508.

Rice, R. E., Gullison, R. E., and Reid, J. W. (1997), „Can sustainable management save tropical forests,“ *Scientific American* 4, 34-39.

Ryan, M. G., Binkley, D., and Fownes, J. H. (1997), „Age-related decline in forest productivity pattern and process,“ *Advances in Ecological Research* 27, 214-262.

Schlenso, M. (1997), "Experimentelle Untersuchungen des Lichtklimas in Urwaldparzellen Nordborneos, No. 117" in *Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen*, Goltze: Göttingen .

Shugart, H. H. (1998), *Terrestrial Ecosystems in Changing Environments*, Cambridge University Press: Cambridge.

Tabarelli, M., Mantovani, W., and Peres, C. A. (1999), „Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil,“ *Biological Conservation* 91, 119-127.

Thomas, S. C. and Bazzaz, F. A. (1999), „Asymptotic height as predictor of photosynthetic characteristics in Malaysian rain forest trees,“ *Ecology* 80, 1607-1622.

Turner, I. M. (1996), „Species loss in fragments of tropical rain forest: a review of the evidence,“ *Journal of Applied Ecology* 33, 200-209.

Turner, I. M., Chua, K. S., Ong, S. Y., Soong, B. C., and Tan, H. T. W. (1995), „A century of plant species loss from an isolated fragment of lowland tropical rain forest,“ *Conservation Biology* 10, 1229-1244.

Warner, R. R. and Chesson, P. L. (1985), „Coexistence mediated by recruitment fluctuations: a field guide to the storage effect,“ *The American Naturalist* 125, 769-787.

Webb, C. O. and Peart, D. R. (1999), „Seedling density dependence promotes coexistence of Bornean rain forest trees,“ *Ecology* 80, 2006-2017.

Whitmore, T. C. (1998, *An introduction to tropical rain forests (2nd edition)*, Oxford University Press: Oxford .

Yasuda, M., Matsumoto, J., Osada, N., Ichikawa, S., Kachia, N., Tani, M., Okuda, T., Furukawa, A., Nik, A. R., and Manokaran, N.), „The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula,“ *Journal of Tropical Ecology* 15, 437-449.