Towards ground-truthing of spaceborne estimates of above-ground biomass and leaf area index in tropical rain forests

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Abstract

The canopy height of forests is a key variable which can be obtained using air- or spaceborne remote sensing techniques such as radar interferometry or lidar. If new allometric relationships between canopy height and the biomass stored in the vegetation can be established this would offer the possibility for a global monitoring of the above-ground carbon content on land. In the absence of adequate field data we use simulation results of a tropical rain forest growth model to propose what degree of information might be generated from canopy height and thus to enable ground-truthing of potential future satellite observations. We here analyse the correlation between canopy height in a tropical rain forest with other structural characteristics, such as above-ground biomass (AGB) (and thus carbon content of vegetation) and leaf area index (LAI). The process-based forest growth model FORMIND2.0 was applied to simulate (a) undisturbed forest growth and (b) a wide range of possible disturbance regimes typically for local tree logging conditions for a tropical rain forest site on Borneo (Sabah, Malaysia) in South-East Asia. It is found that for undisturbed forest and a variety of disturbed forests situations AGB can be expressed as a power-law function of canopy height \( h \) (\( \text{AGB} = a \cdot h^b \)) with an \( r^2 \sim 60\% \) for a spatial resolution of 20 m \( \times \) 20 m (0.04 ha, also called plot size). The regression is becoming significant better for the hectare wide analysis of the disturbed forest sites (\( r^2 = 91\% \)). There seems to exist no functional dependency between LAI and canopy height, but there is also a linear correlation (\( r^2 \sim 60\% \)) between AGB and the area fraction in which the canopy is highly disturbed. A reasonable agreement of our results with observations is obtained from a comparison of the simulations with permanent sampling plot data from the same region and with the large-scale forest inventory in Lambir. We conclude that the spaceborne remote sensing techniques have the potential to quantify the carbon contained in the vegetation, although this calculation contains due to the heterogeneity of the forest landscape structural uncertainties which restrict future applications to spatial averages of about one hectare in size. The uncertainties in AGB for a given canopy height are
here 20–40% (95% confidence level) corresponding to a standard deviation of less than ±10%. This uncertainty on the 1 ha-scale is much smaller than in the analysis of 0.04 ha-scale data. At this small scale (0.04 ha) AGB can only be calculated out of canopy height with an uncertainty which is at least of the magnitude of the signal itself due to the natural spatial heterogeneity of these forests.

1 Introduction

Tropical forests contain about 50% of the carbon stored in the vegetation worldwide (Sabine et al., 2004). Carbon emissions from tropical deforestation are with about 1.5 Pg C yr\(^{-1}\) (years 2000–2007) responsible for 16% of the total anthropogenic carbon emissions. The carbon flux from deforestation in South-East Asia was estimated in 2007 with 0.6 Pg C yr\(^{-1}\) to be as large as that from Latin America (Canadell et al., 2007; Global-Carbon-Project, 2008). These carbon fluxes have estimated uncertainties of around 50% and they are within the global carbon cycle those which are by far the most uncertain ones (Le Quéré et al., 2009). For balancing the global carbon budget in higher accuracy than today, also of interest for Reducing Emissions from Deforestation and Degradation (REDD) within the Kyoto protocol and its successors, it is therefore necessary to reduce the uncertainties contained in the land-atmosphere carbon fluxes.

Our knowledge of the amount of carbon stored in tropical forests is incomplete, but steadily increasing. From tree allometry it is now known that above-ground biomass AGB (and thus carbon contained in the vegetation) might be predicted by trunk diameter or basal area of trees (Chave et al., 2005; Slik et al., 2010), but allometric relations between canopy height and standing biomass are so far missing. Biomass estimates and changes in carbon allocation were calculated from ground measurements for various different areas (e.g. Chave et al., 2003, 2008; Malhi et al., 2006; Lewis et al., 2009; Phillips et al., 2009; Slik et al., 2010). These estimates are restricted to selected research plots and a spatially complete coverage is still lacking.
To overcome the uncertainty in our knowledge of carbon stored in vegetation and to monitor future changes spaceborne remote sensing techniques seems to be the only practical solution. Although various studies used remote sensing for forest characterisation (e.g. Garrigues et al., 2008; Anderson et al., 2009; Bergen et al., 2009; Potter et al., 2009; Frolking et al., 2009; Hawbaker et al., 2009; Dubayah et al., 2010) a region-wide coverage and carbon storage calculation is still missing. This lack of data might be improved by future satellite mission for spaceborne remote sensing of the environment which are now underway (e.g. TANDEM-L or DESDynI – http://desdyni.jpl.nasa.gov – Frolking et al., 2009; Moreira et al., 2009; Hurtt et al., 2010). Therefore, Houghton et al. (2009) laid out the required specifications for these and other future satellite missions to significantly reduce the nowadays existing uncertainties. They claimed, that in order to reduce the uncertainty in the land-atmosphere fluxes to those of the next uncertain term (which is the net carbon uptake of the ocean with an uncertainty of ±18%) a measurement error of less than 2 Mg C (or an AGB uncertainty of about 4 tons organic dry matter, abbreviated \( t \) in the following) per ha over 25 ha is required. It is furthermore argued, that deforestation is patchy on spatial scales of 100 m and less and only if remote sensing is operating on a similar scale, one can clearly identify changes in carbon storage over time and minimise sampling errors due to averaging.

One crucial aspect of remote sensing estimates of vegetation parameters, however, is the validation against reference measurements, so-called ground-truthing. Remote sensing nowadays accurately describes, for example, the height of the canopy (e.g. Lefsky et al., 2002, 2005; Balzter et al., 2007; Hajnsek et al., 2009). To be able to calculate other parameters of the forest (e.g. carbon content) out of the canopy height some well justified assumptions need to be made. In other words some new or modified allometric relationships between canopy height and other structural parameters need to be established. It would therefore be of interest to compare forest inventory data of plots of similar size as the footprint of the satellite with results from remote sensing techniques. This attempt is especially difficult in tropical forest with only about ten globally distributed large research plots of 50 ha in size (Condit, 1995), although the
amount and distribution of field sites was significantly increased during the last years, e.g. in the Amazon (Malhi et al., 2006) or on Borneo (Slik et al., 2009, 2010).

The attempt of this study is to use in the light of restricted field inventories the results of a process-based tropical forest growth model to analyse allometric relationships between canopy height \( h \), a major forest variable measurable from spaceborne remote sensing techniques, and of AGB and leaf area index (LAI), both variables of interest in the research of the carbon cycle and of vegetation dynamics. Accuracy and uncertainties in the calculation of the canopy height during remote sensing are not discussed here. We show from simulations covering the range of disturbances typically found in tropical rain forests in Borneo, how accurate AGB (and thus the carbon content of the vegetation) and LAI can be determined, once the canopy height is known. The analysis is performed on a forest plot level of 20 m \( \times \) 20 m (0.04 ha), representative for typical achievable spatial resolution of spaceborne remote sensing configurations (Frolking et al., 2009), and for larger areas of one hectare (1 ha). The ha-wide averages furthermore enable us to calculate relationships between the degree of canopy disturbance and AGB. Simulation results are finally compared with field data from disturbed and undisturbed forests in Borneo.

2 Methods

2.1 Description of the model

We used the individual-oriented process-based forest growth model FORMIND (Köhler and Huth, 1998) in its updated version FORMIND2.0 (Köhler, 2000) to simulate the forest dynamics of an uneven-aged mixed tropical rain forest. The model has been proven suitable to simulate a wide range of forest sites on Borneo (Sabah) (Köhler et al., 2001), Venezuela (Kammesheidt et al., 2001), French Guiana (Köhler et al., 2003), Mexico (Rüger et al., 2008), Brazil (Groeneveld et al., 2009) and Ecuador (Dislich et al., 2009). The site-specific model adaptation and parameterisation to a dipterocarp tropical rain
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The model describes forest dynamics as a mosaic of interacting forest patches (20 m × 20 m), which have the typical crown size of emergent trees in our observation area. This also implies that the spatial resolution possible with FORMIND2.0 is similar to that of remote sensing estimates (Frolking et al., 2009; Hajnsek et al., 2009). Finer spatial-scale features are not covered by the model. Within these patches trees are not spatially explicitly distributed, and thus all compete for light and space following the gap model approach (Botkin, 1993). 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 discretisation of 0.5 m.

The growth of an individual tree is based on a carbon balance. Calculations include the photosynthesis 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. Photosynthetic production is calculated from the tree’s leaf area. We assume an increasing limitation effect of water transport deficiencies with increasing tree height. Thus, actual productivity is calculated by applying a size-dependent limitation factor. Assimilation losses are estimated in relation to tree biomass. We distinguish between biomass-dependent maintenance respiration and growth respiration. 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. 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. Recruitment takes into account the production and explicit dispersal of individual seeds produced by local mother trees. We assume constant seed input rates which is correlated with the reproductive success at minimum diameter of 1 cm. Thus, the seed production rate lumps together several regeneration stages: fecundity, seed survival, germination and possible predation upon young seedlings. Incoming seeds update a seed pool, taking into account the dormancy variability across functional groups.

We took an undisturbed, primary forest stand (P1) for our stand initialisation from a research inventory in the Deramakot Forest Reserve (DFR) in Sabah (North Borneo, Malaysia, 117°30’ E, 5°25’ N, 130–300 m a.s.l.) (Schlensog, 1997). Deramakot has a per-humid climate typical of the inner tropics. The mean annual temperature is 27°C with little seasonal variation. The average annual precipitation is about 3500 mm, with no pronounced dry season. The geology of Deramakot is characterised by tertiary sediments, mostly sandstone. The soils are low in nutrients and prone to erosion once left devoid of tree cover. The prevailing forest type is lowland dipterocarp forest.

The shrub and tree species found in DFR (total number: 468 species) are assigned to 13 different plant functional types (PFT) based on their successional status and maximum height at maturity (Köhler et al., 2000). The successional status (early, mid, or late) is 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. In FORMIND2.0 thus the life-cycle of individual trees belonging to one of the 13 PFT is calculated.

2.2 Simulated scenarios

Besides the simulation of the evolution of the undisturbed dipterocarp forest (P1) for 400 yr as reference case, we simulated a large number of typical logging scenarios for this region (in total 24 different scenarios, Table 1). The scenarios differ in the logging method responsible for the amount of damage caused in the residual forest stand,
logging cycle (time period between two logging events), and cutting limit \(d_{\text{min}}\) (only trees with a diameter above the cutting limit are logged). The size of the simulated forest area was kept constant at 100 ha and we assumed the boundary conditions to be periodic. The length of simulation in the logging scenarios was 240 yr.

Our modelling of logging methods was motivated by several studies, but see references and more details in Huth et al. (2004, 2005). We distinguish two methods: highly damaging conventional logging (CON), which generally uses heavy machinery and unskilled workers, but little planning, 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 airborne cable systems. The differences modelled between the two methods represent the logging impact on the residual stand. The time between two logging operations was constant, but differed between the scenarios (20, 40, 60, 80 years). All commercial trees of the mid- and late-successional species above the cutting limit \(d_{\text{min}}=40, 50, 60 \text{ cm}\) were removed in a logging operation.

The simulated forests were analysed over the whole simulated area \(A\) (in ha) over the whole simulation periods \(T\) (in yr) with outputs produced every year including one initial output at \(t=0\) yr. Thus, we can rely for every simulation on \((T+1)\times A\) data sets of ha-wide mean averages and on \((T+1)\times A\times 25\) on detailed 0.04 ha plot-related informations. These are 40 100 (ha) and 1 002 500 (0.04 ha) data sets for the 400 yr runs of P1 and 24 100 (ha) and 602 500 (0.04 ha) data sets for each logging scenario. For the latter, some additional data sets directly after each logging event might be added to them. If we finally average over all disturbed forests we end up with 578 000 or 14 460 000 data sets for the ha and plot related informations, respectively. On average, the simulated undisturbed and disturbed forests contained 2795 and 3202 trees per hectare, respectively.

In the simulated forests we analysed at different spatial scales (0.04 or 1 ha) the relationship between (a) canopy height \(h\) and AGB and (b) canopy height \(h\) and LAI. Canopy height is defined as the height of largest tree on the plot scale (0.04 ha), and
as the mean height of the largest trees of the 25 individual plots of each ha on the 1 ha-scale. Additionally, at the 1 ha-scale the relationship between the gap fraction and AGB is analysed. Gap fraction is here defined as the fraction of the simulated forest area with a canopy height \( h \) below 25 m.

2.3 Permanent sampling plots data from Sabah and large-scale field inventory from Lambir

The data from permanent sampling plots (PSPs), with which we compared our simulation results, were collected in five different forest reserves in Sabah, Malaysia between 1973 and 1993. The data are described and analysed in Köhler et al. (2001). PSPs are between 1 and 11 ha large, contain more than 12 000 trees, which were sampled between 9 and 20 years in intervals of 1 to 5 years. All plots were regrowing forests in which during their first inventory the last logging event was 8 to 45 years ago. The PSP data therefore cover forest regrowth 8 to 54 years after disturbance. The data consist of repeated measurements of diameter at breast height (dbh). AGB is calculated out of dbh with the allometric relationship and species grouping embedded in FORMIND2.0.

The large-scale (52 ha) field inventory at Lambir covers one initial sampling of biomass per 0.04 ha plot (Yamakura et al., 1996). This forest is believed to be largely undisturbed by anthropogenic activities and might therefore be a representative for an undisturbed rain forest site on Borneo. However, please note, that the parameterisation of our model was not optimised for Lambir (Sarawak, Borneo), and differences in detail are therefore expected. The Lambir data set is nevertheless the largest forest inventory in South-East Asia comparable to the undisturbed dipterocarp forest in DFR used for parameterisation and initialisation of our simulation. However, besides the biomass distribution data used here other raw data were not available to us.
3 Results

3.1 Undisturbed tropical rain forest

In the simulation of undisturbed tropical rain forest only natural gap creation by falling large trees occurs, neither anthropogenic tree extraction nor external disturbances, such as storms, are considered. These simulations are potential representations of forest development (potential natural vegetation dynamics) in the remote interior of Borneo.

If analysed on the forest plot level (0.04 ha) AGB can be predicted from canopy height $h$ using a power-law function $\text{AGB} = a \cdot h^b$ with an $r^2 = 61.4\%$ (Fig. 1A). Linear or quadratic function are with a correlation coefficient of 58.9% and 60.8%, respectively, only slightly worse than the power-law equation. The spread in AGB data for a given canopy height is large. The relative uncertainty on the 95% confidence interval ($4 \sigma$/mean) is larger than 100% for trees smaller than 26 m and generally larger than 200% for $h$ smaller than 12 m (Fig. 1D). The relative uncertainty is with 80–85% stable for canopy heights between 30 and 45 m and declines towards 20% for plots with canopy heights of 50 m. The decline in relative uncertainty for canopies larger than 45 m might be caused by the low sample size. Only very few tree species, or PFTs, can grow to such heights, thus reducing the variability. To summarise, the variability of biomass growth underneath the largest growing tree within a plot is in tropical rain forests huge and a simple back calculation without additional information from canopy height to standing stock at this scale is ambiguous.

In the 1 ha-scale analysis regressions between AGB and $h$ are with $r^2 = 58\%$ of similar quality than for the plot-size (0.04 ha-scale) (Fig. 2). However, uncertainties in the prediction of AGB as functions of $h$ are much smaller. Canopy height, now represented as ha-wide averages, varied only between 35 and 42 m, the relative uncertainty was stable at 18–20% throughout the range of $h$ (95% confidence level).

As large-scale inventories of undisturbed forest sites are lacking in Sabah we restrict the comparison of simulation results to the large-scale inventory of the Lambir forest
reserve in the Malaysian province Sarawak on Borneo. In the biomass distribution of the 1 ha-scale from the 52 ha inventory in Lambir (Yamakura et al., 1996) the frequency maxima of 541 t/ha is very close to 545 t/ha of our undisturbed forest simulations P1 (Fig. 3). The distribution is wider for Lambir in both spatial scales, probably due to the sampling size which was nearly three orders of magnitude smaller in the field data (n=40 100 or 52 ha for simulations and Lambir, respectively). This comparison is therefore restricted, but it shows that the biomass distribution of the simulated rain forest is within the range seen in real forest inventories, and strongly depends on the spatial scale.

3.2 Logged (disturbed) tropical rain forest

For the logged forests some interesting patterns emerged. The number of forest plots with large canopy heights is strongly reduced. The maximum in the AGB distribution in the plot (0.04 ha) scale is shifted from 500 t/ha in the undisturbed to 300 t/ha in the disturbed forests (Fig. 4B). Similarly, canopy height is reduced from a maximum in the distribution at 42 m to 37 m (Fig. 4C). In the PSPs the distribution is shifted to even smaller canopies (maximum at ~30 m height) with less biomass (maximum ~100 t/ha). This indicates, that the PSP data do not cover the same range as the simulated disturbed forests, but are biased towards smaller, heavier disturbed sites. This bias is based on the fact, that the PSP data are restricted to 8–54 years after tree extraction. They are thus not representative for disturbed forest dynamics with long cutting cycles (60–80 years), although these conditions are found in 50% of our logging scenarios.

On the 0.04 ha-scale regressions are with an $r^2$ of about 60% of similar quality for undisturbed and disturbed forests simulations as well as for the PSP data, although the power-law equations differ in detail (Fig. 4A, Table 2). The relative uncertainty on the 95% confidence level is slightly worse for the disturbed forests and the PSP data than for the undisturbed site P1, but both repeat the general pattern of the undisturbed forests (Fig. 4D).
On the larger spatial scale of ha-averages the power-law regression equation leads in the disturbed forest simulations as well as in the PSP data to significantly better agreement with the underlying data ($r^2=90$ and 91%, respectively) than in the undisturbed simulations (58%) (Fig. 5A). One can clearly identify in the scatter plot of AGB over $h$ (Fig. 5A), that the undisturbed simulations are only a subsample at the upper end of the disturbed forest simulations. Furthermore, the PSP data represent the lower range of the disturbed forest simulations. The scatter of disturbed forest data points for AGB<200 t/ha and canopy height $h\sim32$ m (Fig. 5A) is caused by the appearance of pioneer PFT after logging operations. They dominate the plots for some years, before in the secondary successions other PFTs take over. However, because of their low wood densities these pioneers are rather unimportant for the calculation of mean above-ground biomass. The relative uncertainty at the 95% confidence level is larger than 40% in the disturbed forests for canopies smaller than 25 m, and between 20 and 40% for larger canopies and throughout the PSP data set (Fig. 5B).

There is no significant correlation between LAI and canopy height ($r^2<5\%$), neither in the undisturbed nor in the disturbed forest simulations, neither on the smaller 0.04 ha-scale (Fig. 6A) nor on the large 1 ha-scale (Fig. 6B). Again, PSP data are on the lower end of the range of the simulated data.

A linear relationship with an $r^2$ of 58% can be obtained from the 1 ha-scale analysis of AGB as function of gap fraction (Fig. 7A). Here, gaps are defined as 20 m×20 m plots with a canopy height below 25 m. In all logging simulations there are areas with low gap fraction (typically <15%) and with high gap fraction (around 25% for reduced-impact logging RIL, and above 40% for conventional logging CON), the range in-between is somehow not covered at all (Fig. 7B). This might be understood as the following: The high gap fractions are a direct result of the logging operations. Directly after logging the fast growing pioneer PFT grows first in these highly disturbed gap areas, and below them other trees species get established. Because logging disturbed the whole simulation area at the same time the closure of the forest canopy last as long as the growing of these pioneer trees to 25 m height (threshold of the definition of a forest gap), and
will thus happen more or less simultaneously in all plots which were disturbed by the logging operation. Each disturbance regime produces its own typical pattern in a AGB-gap fraction diagram (Fig. 7B). This is a first indication that such patterns might be detectable by remote sensing in the future to distinguish different disturbance regimes in tropical forests from air- and spaceborne observations.

4 Discussion and conclusions

To reduce the uncertainties in our knowledge of the carbon cycle a global coverage of the terrestrial carbon storage is a desirable target, for which spaceborne remote sensing techniques have to be applied. Repeated annual measurements could thus identify large sources and sinks of carbon due to large-scale deforestation or reforestation programs.

Within this effort a knowledge of the uncertainties and at best their minimisation is crucial to determine whether or not new approaches might improve our knowledge of the terrestrial carbon storage and its variability over time. It was already shown, how error propagates in inventory-based biomass estimates in tropical forests, in which AGB is typically derived from allometric relationship with the stem diameter of individual trees and only seldomly measured directly (Chave et al., 2004). Another huge uncertainty on the way to a complete carbon balance of tropical forests is the amount of carbon bound in dead wood, so-called necromass, above ground (Chao et al., 2009) and in forest soils below ground (Luyssaert et al., 2008). Both pools are largely unsampled, but might introduce due to their relatively small size in the tropics (Bonan, 2008) and due to their linear relationship with AGB only a small bias to the overall carbon budgets (Cairns et al., 1997).

If AGB is calculated not as a function of tree diameter known to be the best predictor of AGB (Chave et al., 2005; Slik et al., 2010), but from more aggregated variables such as canopy height, we implicitly pay for such an AGB estimate on the cost of precision. Remote sensing approaches are the only practical solution for a large-scale
systematic vegetation monitoring. There is a need to establish new allometric relationships for tropical forests. In the absence of field inventories covering all possible forest situations forest growth models are useful tools to derive such new relationships. This is especially the case for uneven-aged mixed forest stands in the tropics in which long logging cycles are necessary for sustainable timber harvesting. The simulation results can not completely compensate for inventories, but they can significantly broaden the spectra of possible forest situations on the plot level.

Another advantage of forest growth modelling is the consistency of the analysed set of simulation results. The FORMIND2.0-model does not account for uncertainties in the allometric relationships between dbh and AGB and reduces species-specific differences to the 13 PFT, which were selected for Borneo’s rain forest. Thus, the uncertainties we here calculate are structural uncertainties between the aggregated variables canopy height $h$ and AGB and LAI. They might in detail differ in field inventories, but they are in principle contained in the vegetation structure of tropical rain forests.

We therefore conclude that the structural uncertainties in AGB estimates based on given spaceborne canopy height measurements are according to our simulations results (and in agreement with PSP data) on the order of 20–40% if ha-wide averages are investigated (95% confidence level). However, for the calculation of the overall uncertainty of AGB the accuracy of the canopy height derived from remote sensing techniques must also be taken into consideration. Canopy height estimates obtained from airborne polarimetric interferometric synthetic aperture radar (Pol-InSAR) or airborne LIDAR over dipterocarp tropical rain forests have shown, that the mean canopy height of the hundred largest trees on one hectare can be measured with an accuracy of 10% ($\sigma$) (Hajnsek et al., 2009). It therefore seems possible that the suggested target of maximum uncertainty of $\pm 18\%$ for AGB given by Houghton et al. (2009), equivalent to an uncertainty of 36% (95% confidence level), can be reached. Our study shows that this would apply to tropical rain forest sites of nearly all disturbance regimes, if the aggregated information on the 1 ha-scale are used for the analysis. On the plot level (0.04 ha-scale) the uncertainties in $\text{AGB}=f(h)$ are as large as or larger than the signal.
itself. The uncertainty can be reduced if it would be possible to derive information on the vertical forest structure by remote sensing techniques in the future. According to our analysis the LAI can not be predicted from canopy height.

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References


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Table 1. Simulation scenarios. Undisturbed site P1 or different logging scenarios with disturbed forests.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Logging method</th>
<th>Logging cycle (yr)</th>
<th>Cutting limit (cm)</th>
<th>Simulation period $T$ (yr)</th>
<th>Area $A$ (ha)</th>
<th>Plots $n$ (400 m$^2$)</th>
<th>runs</th>
<th>tree density (1/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1 (undisturbed)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>400</td>
<td>100</td>
<td>2500</td>
<td>1</td>
<td>2795</td>
</tr>
<tr>
<td>Logging (disturbed)</td>
<td>RIL, CON</td>
<td>20, 40, 60, 80</td>
<td>40, 50, 60</td>
<td>240</td>
<td>100</td>
<td>2500</td>
<td>24</td>
<td>3202</td>
</tr>
</tbody>
</table>
**Table 2.** Regression functions between above-ground biomass AGB (per plot or as ha-mean) and canopy height \( h \) or gap fraction (gap: maximum height of plot < 25 m) of site for undisturbed site P1 or average over all 24 logging scenarios.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Function</th>
<th>( r^2 )</th>
<th>Function</th>
<th>( r^2 )</th>
<th>Function</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1 (undisturbed)</td>
<td>( y = 0.15 \cdot x^{2.23} )</td>
<td>61.4%</td>
<td>( y = 0.52 \cdot x^{1.89} )</td>
<td>58.1%</td>
<td>( y = 548 - 7.13 \cdot x )</td>
<td>1.7%</td>
</tr>
<tr>
<td>Logging (disturbed)</td>
<td>( y = 0.44 \cdot x^{1.89} )</td>
<td>58.0%</td>
<td>( y = 0.07 \cdot x^{2.42} )</td>
<td>90.6%</td>
<td>( y = 394 - 4.95 \cdot x )</td>
<td>58.3%</td>
</tr>
</tbody>
</table>
Fig. 1. Relation between above-ground biomass (AGB) and canopy height ($h$) for the undisturbed forest (site P1). (A) Data on 0.04 ha-scale (grey to black) (red: 1 ha-scale for comparison) are plotted together with a power-law regression function. Due to the huge number of data points in the scatter plot of the 0.04 ha-scale (more than 1 000 000) the grey-scale indicates the density of the data points with highest densities in black. Normalised density of (B) AGB and of (C) $h$ for both spatial scales. Legend in (C) as in (B) and (D): Relative uncertainty (4 σ/mean) of the 95% confidence interval, dotted horizontal line marks unity.
Fig. 2. Relation between above-ground biomass (AGB) and canopy height \((h)\) in 1 ha-scale analysis for the undisturbed forest (site P1), including power-law regression function. Relative uncertainty \((4\sigma/\text{mean})\) of the 95% confidence level plotted on right \(y\)-axis.
Fig. 3. Comparison of the normalised frequency distribution of above-ground biomass for (A) undisturbed forests (site P1) with (B) field data from the large-scale inventory of 52 ha in Lambir, Sarawak, Malaysia (Yamakura et al., 1996) for both 0.04 and 1 ha-scale. P1 simulations were already plotted in Fig. 1B. P1 simulations cover 100 ha with annual output over 400 yr \(n=40100\), while the Lambir field data cover one inventory over 52 ha \(n=52\). The larger data ensemble of the simulations therefore enable a finer discretisation of AGB than the Lambir field data \(\Delta(AGB)=10\) and 100 t/ha, respectively.)
Fig. 4. Regression lines of above-ground Biomass (AGB) and canopy height (h) in 0.04 ha-scale composition for the undisturbed forest (site P1), for disturbed forests (all 24 logging scenarios), and for permanent sampling plot (PSP) data. The scatter plot of undisturbed (see Fig. 1) and disturbed forests are indistinguishable due to overlap and the data from the undisturbed site P1 are therefore omitted. Due to the huge number of data points in the scatter plot of the 0.04 ha-scale (more than 14 000 000) the grey-scale indicates the density of the data points with highest densities in black. Normalised density of (B) AGB and of (C) h and relative uncertainty (D) on the 95% confidence level (4 σ/mean) are plotted for disturbed and undisturbed forest and PSP data, legend as on (A).
Fig. 5. (A) above-ground biomass (AGB) and canopy height ($h$) in 1 ha-scale composition for the undisturbed site P1 (red), for disturbed forests in all 24 logging scenarios) (green), and for permanent sampling plot (PSP, blue) data. (B) Relative uncertainty on the 95% confidence level ($4 \sigma$/mean), legend as in (A).
Fig. 6. Relation between leaf area index (LAI) and canopy height ($h$) on the (A) 0.04 ha-scale and (B) 1 ha-scale. Results for the undisturbed site P1, for disturbed forests (all 24 logging scenarios, and for permanent sampling plot (PSP) data. In sub-figure (A) only disturbed (logged) forests and PSP data are shown, because the scatter plot for the undisturbed forest (P1) is indistinguishable from the disturbed forest data. Due to the huge number of data points in the scatter plot of the 0.04 ha-scale (more than 14 000 000) the grey-scale indicates the density of the data points with highest densities in black.
Fig. 7. Relation between above-ground biomass (AGB) and gap fraction. Gaps are defined as individual 20 m × 20 m plots with canopy height \( h < 25 \) m. (A): Undisturbed forest P1 (red), disturbed forests of all logging scenarios (green), and permanent sampling plot (PSP, blue) data. (B): Two specific examples for logging are highlighted: Cyan: reduced-impact logging (RIL), 80 y return interval, minimal dbh of logged trees =60 cm. Magenta: conventional logging (CON), 20 y return interval, minimal dbh of logged trees =40 cm.