THE EFFECTS OF LOGGING ON THE ARCHITECTURE OF BORNEAN RAIN FOREST TREES

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Received May 2002

STERCK, F. J., HILLE RIS LAMBERS, R. & BONGERS, F. 2003. The effects of logging on the architecture of Bornean rain forest trees. Tree parameters were compared between trees in a logged (logged eight years ago) and an unlogged forest in Borneo. This comparison was made for 3 to 10 cm diameter at breast height (dbh) trees of four tree species, namely, Mallotus penangensis, M. urayi, Shorea johorensis and S. parvifolia. The crown position index indicated that light levels tended to be lower in the logged forest. This probably resulted from the higher tree densities in the 10 to 30 cm dbh class. Leaf display parameters did not differ between the forests. Logged forest trees had narrower crowns than unlogged forest trees, except for M. urayi. Mallotus urayi and S. parvifolia had relatively thick boles in logged forest. These responses to logging may reflect recent competition for light and space (narrow crowns), and high light levels shortly after logging (thicker boles). These architectural responses to logging did not parallel architectural responses to increased light levels. After eight years the canopy of the logged forest had already closed, and light levels above juvenile trees were low. This indicated that the effects of increased light levels quickly reduced during the first years after logging.

Key words: Borneo - crown - Dipterocarpaceae - Euphorbiaceae - light - morphology


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Introduction

Tropical rain forests are being logged at fast rates worldwide, and logged tropical forests occupy increasingly large areas every year (McNeely et al. 1990). Logging affects regeneration, structure, and composition of the tree community (de Graaf 1986, Silva et al. 1995). The recovery of the forest mainly depends on (1) the establishment of a new generation of viable seeds and propagules, as determined by the presence of reproductive trees, and potential pollinators and seed dispersers (Janzen & Vázquez-Yanes 1991, Bruenig 1993, Jansen & Zuidema 2001) and (2) the consequences of the modified growth conditions for the remaining stand and, in more particular, for the physiological and architectural parameters underlying tree performance (Ter Steege et al. 1994, Tuomela et al. 1996, Guariguata & Dupuy 1997, Zagt 1997). In this study, the effects of logging on architectural parameters (tree shape and leaf display) were investigated in several tree species of a Bornean rain forest and, based on the results, a hypothesis was formulated for the forest recovery process after logging.

Of the modified growth conditions after logging, the change in light intensity probably has the greatest impact on architectural parameters. Large gaps emerge where big trees are harvested, and considerably increase the frequency of high light levels in the forest. Trees surviving logging thus have greater probability to encounter high light levels, and to escape light suppression, than do trees in unlogged forests. Some studies show that the effects of logging on architectural parameters are similar to the effects of large natural canopy gaps, and thus suggest that these effects indeed result from increasing light levels or accompanied changes in factors such as temperature, relative humidity and wind speed (e.g. Ter Steege et al. 1994, van der Meer 1995). It has been shown that juvenile trees generally respond to higher light by producing (1) bigger crowns with more leaf layers per crown area, enhancing crown photosynthesis at high light while reducing leaf self-shading at low light, and (2) thicker boles, improving stability and water transport in more exposed conditions (Horn 1971, Holbrook & Putz 1989, King 1994, Bongers & Sterck 1998, Sterck 1999). Such architectural responses are shared by species differing in life history, and they reflect faster growth and higher investments in bole diameter rather than height increment at high light intensity levels (Sterck et al. 2001). In response to the high light levels following logging, we expect that architectural parameters of different tree species respond to logging in the same direction as to light. This work hypothesis is tested for four tree species of a Bornean lowland rain forest.

Materials and methods

Site and species

The study was performed at the Danum Valley Field Centre, Sabah, Malaysia. This site is characterised by humid warm climate with temperatures between 18 (morning) and 35 °C (afternoon), and an annual rainfall between 2500 to 3000 mm.
The forest has been classified as the \textit{Parashorea malaanonan} type by Fox (1972), and is dominated by dipterocarps in the overstorey and euphorbs in the understorey (Newbery \textit{et al.} 1992, 1996).

In 1996, 10 study plots (40 X 40 m) were established at random locations on ridge and slope sides (and not in valleys) in a 100-ha logged forest, and 10 control plots were established in the same way in an unlogged forest. The plots were inventoried for trees with a minimum girth of 10 cm at breast height (dbh > 3.1 cm) in 1996. All trees were identified to species. The logged forest was logged intensively eight years earlier (1988). Commercial trees with a dbh > 60 cm were harvested and extracted with tractors (Schnaeckel 1996).

Four common tree species were selected for further study, namely, \textit{Mallotus wrayi}, \textit{M. penangensis} (Euphorbiaceae), \textit{Shorea johorensis} and \textit{S. parvifolia} (Dipterocarpaceae). Both euphorbs are understorey species and have low growth rates and low mortality rates (Table 1). Both dipterocarps are overstorey species and have high growth rates and high mortality rates (Table 1). These species were selected because they represented the two dominant families and life history groups of these forests (Newbery \textit{et al.} 1992, 1996), and occurred in large numbers in the study plots.

\textbf{Table 1} Life history parameters for the four study species, using data from two 4-ha plots of a tropical rain forest at Danum Valley Field Centre, Sabah, Malaysia\textsuperscript{*}

<table>
<thead>
<tr>
<th>Species</th>
<th>Bole\textsuperscript{1}</th>
<th>Maximum stature</th>
<th>Bole increment</th>
<th>Mortality rate</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bole\textsuperscript{1}</td>
<td>Maximum stature</td>
<td>Bole increment</td>
<td>Mortality rate</td>
<td>N</td>
</tr>
<tr>
<td></td>
<td>Dbh</td>
<td>Height</td>
<td>Medium</td>
<td>Maximum\textsuperscript{2}</td>
<td>(10\textsuperscript{-2}/year)</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{Mallotus wrayi}</td>
<td>P</td>
<td>0.17</td>
<td>17</td>
<td>0.39</td>
<td>1.28</td>
</tr>
<tr>
<td>\textit{M. penangensis}</td>
<td>O</td>
<td>0.23</td>
<td>21</td>
<td>0.57</td>
<td>1.59</td>
</tr>
<tr>
<td>Dipterocarpaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{Shorea johorensis}</td>
<td>O</td>
<td>1.27</td>
<td>55</td>
<td>4.40</td>
<td>10.01</td>
</tr>
<tr>
<td>\textit{S. parvifolia}</td>
<td>O</td>
<td>1.21</td>
<td>49</td>
<td>6.66</td>
<td>14.09</td>
</tr>
</tbody>
</table>

\textsuperscript{1} P= plagiotropic, O = orthotropic, \textsuperscript{2} 95 percentile value, thus correcting for outliers

\textsuperscript{*}Adapted from Sterck \textit{et al.} 2001. Mortality rate and bole diameter increment have been calculated over a five-year period for all trees with a dbh between 3.1 and 19.0 cm. Mortality was calculated following Sheil \textit{et al.} (1995).

\textbf{Field measurements}

Individuals were measured in logged and unlogged forest in November till December 1996. For the period between 1988 (logging event) and 1996 there were no data available for tree site or tree architecture. The presented data are results obtained from measurements made in 1996 only. Individuals with bole decreasing abruptly in width (> 50\%) were considered severely damaged and were excluded. Of all inventoried individuals, between 7 and 22\% were considered damaged. Of the undamaged individuals, two individuals were selected randomly for each cm-class between 3 and 10 cm dbh (3–4 cm, 4–5 cm, etc.). The individual
plots were not included as a selection criterion, since this would further reduce our sample size. In this way, 14 individuals were selected per species in both the logged and the unlogged forest.

Tree height and the height of the lowest leaf were measured using a 16-m high telescopic measuring pole (precision ± 10 cm). Crown radii were measured in eight directions (north, north-east, east, etc.), using a Suunto and compass (precision ± 10 cm). The following tree parameters were calculated: crown depth/width ratio, crown width/tree height ratio, crown depth/tree height ratio, tree height/dbh ratio, and crown area.

The number of leaf layers was determined at five random locations. The telescoping measuring pole (up to 16 m) was pushed up and the number of "leaf hits" was counted. Leaf cover, i.e. the area occupied by leaves in the horizontal crown projection, was estimated visually. Five classes were used: (1) 0–20% covered by leaves (2) > 20–40%, (3) > 40–60%, (4) > 60–80%, and (5) > 80–100%. Data from another study (Sterck et al. 2001) were used for the calculation of total leaf area using regression: ln (total leaf area) = 0.70 ln (product of number of leaf layers, leaf cover and crown area) (F = 206, df = 62, r² = 0.77, p < 0.0001).

Three site descriptors were determined for each tree, each of these descriptors being correlated either to light level, available space, or both. Firstly, the crown position index was estimated visually for each tree (Clark & Clark 1992). This index includes seven classes:

1 = no direct light, i.e. not exposed to canopy openings,
1.5 = low lateral light, i.e. one to few small lateral canopy openings,
2.0 = medium lateral light, i.e. a larger number of small lateral canopy openings,
2.5 = high lateral light, i.e. one or more large lateral canopy openings,
3 = some overhead light, i.e. canopy opening above crown between 10–90%,
4 = full overhead light, i.e. canopy opening above crown > 90%, and
5 = crown completely exposed, i.e. no canopy both vertically and laterally.

This measure is strongly correlated to light availability (Clark et al. 1993). Secondly, the amount of open space above the crown was quantified, using three classes: (1) less than 1 m free space above at least half of the crown area, (2) more than 1 but less than 5 m free space above at least half of the crown area, and (3) more than 5 m free space above at least half of the crown area. In order to measure "open space" the telescopic pole was pushed upwards, and heights were read at the top of the crown and at the bottom of the first overtopping crown.

Finally, the canopy height of the forest above the individual was determined, using a range-finder. Five canopy height classes were distinguished: (1) < 10 m, (2) 10–< 20 m, (3) 20–< 30 m, (4) 30–< 40 m, and (5) > 40 m (for more details on methodology, see Sterck et al. 2001).
Analysis

Tree sites were compared between logged forest and unlogged forest trees. Individuals were matched on the basis of their dbh (N = 14 pairs per species); paired individuals varied between 0.1 and 0.6 cm in dbh. The tree site descriptors were compared between logged forest and unlogged forest trees, using a chi-square test with a Yates correction. Differences in tree site may result from different tree densities; therefore, frequencies of all trees present in the logged and unlogged forest plots were compared (chi-square test). These analyses were done for trees of the same size as the trees selected for architectural measurements (dbh = 3–10 cm), and for larger trees (dbh 10–30 cm, and > 30 cm). Ultimately, architectural parameters were compared between trees in the logged and the unlogged forest, using the Wilcoxon matched pair test (two-tailed).

Results

Tree site

Trees of logged and unlogged forest did not differ significantly in the amount of available space (Table 2). Forest canopy height tended to be lower for the logged forest, but not significantly (p = 0.10). At the species level we did not find differences in crown position index. However, when all species were pooled, logged forest trees had lower crown positions than the unlogged forest trees (p < 0.05). In addition, the 10–30 cm trees were more abundant in logged forest (Figure 1), and probably accounted for the low crown position index of our selected logged forest trees.

![Figure 1](image)

Figure 1  A frequency diagram of trees in logged (dashed bars) and unlogged forest (open bars). Mean frequencies are shown for a 40 × 40 m plot (N = 10). The frequency of 10–30 cm dbh trees was highest in the logged forest plot (t = 2.8, df = 9, p < 0.05, two-tailed, Chi-square test), while frequencies of the other two size classes did not differ significantly between forests. Standard deviations are indicated.
Architecture

The leaf display parameters (total leaf area, number of leaf layers, leaf cover) did not differ significantly between logged forest and unlogged forest trees (Table 3). Tree height/bole diameter ratios were lower in the logged forest in *M. urayi* and *S. johorensis*, but not in the other two species. The crown depth to width ratio was greater in the logged forest for *M. penangensis* and *S. parvifolia*. *Shorea johorensis* had lower crown depth/tree height ratio in the logged forest. Also, the crown width/tree height ratio tended to be lower in the logged forest, though not significantly (*p* = 0.06). *Mallotus urayi* did not show significant patterns for crown allometry.

Discussion

The architectural responses to logging did not parallel the architectural responses found in response to increased light levels. Apparently, the conditions that the trees responded to were more complex than a simple increase in light and associated factors. Consequently, on the basis of our results we present a hypothesis for the light conditions that trees encountered during the eight years between logging and period of measuring tree architecture. The architectural patterns are discussed in terms of responses to these light conditions and correlated factors over eight years.

*Environmental change after logging: a hypothesis*

Juvenile logged forest trees (3–10 cm dbh) were less exposed than unlogged forest trees, which is in contrast with the expectation that logged forest trees receive more light. The logged forest juveniles seemed heavily shaded by the high tree densities in the 10–30 cm dbh class. Pioneer trees, in particular those belonging to the genus *Macaranga*, which probably established shortly after the logging event, accounted for the high densities in the 10–30 cm dbh class of logged forest (Schnaeckel 1996).

From these patterns we suggest a scenario in four steps for the forest and light dynamics in the eight years after logging:

1. Logging operations typically reduced tree numbers in all size classes, the big ones being harvested and many small ones being damaged, and thus created high light levels in the more open sites (Johns 1988, Grieser Johns 1997, Ter Steege *et al.* 1994).

2. Pioneer trees established in open sites shortly after logging. As a number of *Macaranga* species are considered large gap and secondary succession specialists (Davies *et al.* 1998), the high densities of *Macaranga* trees suggest that large gaps were indeed abundant, and colonised, after logging (Silva *et al.* 1995, Kuusipalo *et al.* 1996).
Table 2  Tree site descriptors of four tree species are compared between logged forest and unlogged forest trees at Danum Valley, Sabah, Malaysia

<table>
<thead>
<tr>
<th>Tree site</th>
<th>Range</th>
<th>Mallotus penangensis</th>
<th>M. wrayi</th>
<th>Shorea johorensis</th>
<th>S. parvifolia</th>
<th>All species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Unlogged (%)</td>
<td>Logged (%)</td>
<td>Unlogged (%)</td>
<td>Logged (%)</td>
<td>Unlogged (%)</td>
</tr>
<tr>
<td>Crown position</td>
<td>(&lt; = 2.5)</td>
<td>64 79</td>
<td>86 79</td>
<td>42 71</td>
<td>57 71</td>
<td>63 75*</td>
</tr>
<tr>
<td>Canopy height</td>
<td>(&gt; = 4)</td>
<td>64 50</td>
<td>57 50</td>
<td>50 36</td>
<td>57 57</td>
<td>57 48</td>
</tr>
<tr>
<td>Space</td>
<td>(=1)</td>
<td>71 57</td>
<td>43 50</td>
<td>29 43</td>
<td>43 36</td>
<td>46 46</td>
</tr>
</tbody>
</table>

Note: * = Significant difference at p < 0.05. The difference in canopy height for all species pooled came close to significance (p ~ 0.10).

Table 3  Architectural parameters of four tree species compared between logged and unlogged forest at Danum Valley, Sabah, Malaysia

<table>
<thead>
<tr>
<th>Tree parameter</th>
<th>Prediction</th>
<th>Mallotus penangensis</th>
<th>M. wrayi</th>
<th>Shorea johorensis</th>
<th>S. parvifolia</th>
<th>Pool</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Unlogged Log</td>
<td>Unlogged Log</td>
<td>Unlogged Log</td>
<td>Unlogged Log</td>
<td>Unlogged Log</td>
</tr>
<tr>
<td>Crown depth/crown width</td>
<td>+</td>
<td>2.16 2.65*</td>
<td>1.22 1.12</td>
<td>0.84 0.77</td>
<td>1.05 1.41*</td>
<td>*</td>
</tr>
<tr>
<td>Crown width/tree height</td>
<td>+</td>
<td>0.32 0.27*</td>
<td>0.34 0.38</td>
<td>0.33 0.29</td>
<td>0.29 0.27*</td>
<td>*</td>
</tr>
<tr>
<td>Crown depth/tree height</td>
<td>+</td>
<td>0.64 0.67</td>
<td>0.42 0.41</td>
<td>0.27 0.20*</td>
<td>0.30 0.52</td>
<td></td>
</tr>
<tr>
<td>Tree height/bole diameter</td>
<td>-</td>
<td>1.50 1.67</td>
<td>1.39 1.16*</td>
<td>1.50 1.42*</td>
<td>1.58 1.53</td>
<td>*</td>
</tr>
<tr>
<td>Total leaf area (m²)</td>
<td>+</td>
<td>5.92 5.79</td>
<td>4.46 5.00</td>
<td>4.26 3.74</td>
<td>4.03 4.36</td>
<td></td>
</tr>
<tr>
<td>Number of leaf layers</td>
<td>+</td>
<td>3.24 3.77</td>
<td>1.89 2.47</td>
<td>1.91 1.71</td>
<td>1.96 2.74</td>
<td></td>
</tr>
<tr>
<td>Leaf cover (%)</td>
<td>+</td>
<td>61.40 53.60</td>
<td>49.20 48.60</td>
<td>45.00 42.20</td>
<td>38.60 47.20</td>
<td></td>
</tr>
</tbody>
</table>

Mean values of logged vs. unlogged forest trees are presented. Predictions are + when logged forest trees were expected to have larger parameter values than unlogged forest trees, and - when lower values were expected for logged forest trees. Significant differences (p < 0.05) are indicated with * (Wilcoxon matched-pairs test, two-tailed). Note that most tree parameters are dimensionless.


