Limited Edge Effects Along a Burned-Unburned Bornean Forest Boundary Seven Years after Disturbance

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ABSTRACT

Large parts of the everwet tropics have been burned, leaving many unburned–burned forest edges. Here we studied a Bornean forest edge to determine: (1) how unburned and burned forest differ in vegetation structure, diversity, composition and plant functional traits 7 yr after fire, and (2) if these variables showed significant edge effects. Environmental and inventory data from 120 plots (0.01 ha each), covering both sides of a ~1.3 km forest boundary were sampled. Differences in vegetation structure, diversity, composition and plant functional traits were analyzed in relation to disturbance type (Mann–Whitney tests) and edge distance (partial correlation analysis that controlled for confounding effects of elevation, slope and fire intensity). Seven years after fire, burned forest differed significantly from unburned forest in most measured variables while few significant edge effects were detected, i.e., there existed a sharp delimitation between the two forest types. The regeneration of the burned forest depended almost entirely on in situ recruitment with little input of late successional species from the neighboring old growth forest. On the other hand, old growth forest showed few signs of edge degradation. A possible explanation for these results might be related to the absence of a mast fruiting event during these first 7 yr of forest recovery, resulting in low levels of late successional species seed input into the burned forest, combined with the quick development of a closed canopy in the burned forest by early successional species that shielded the unburned forest from adverse edge effects.

Key words: canopy development; dispersal limitation; functional traits; mast fruiting; regeneration; tropical forest fire.

Tropical forests have become increasingly fragmented in recent decades, resulting in a huge increase in forest edge length and associated edge dynamics (Didham & Lawton 1999, Laurance et al. 2002, Broadbent et al. 2008). Many studies have shown that old growth forests near these margins can experience serious degradation (Laurance et al. 2006a, b, Tabarelli et al. 2008), raising the troubling prospect of an accelerating erosion of undisturbed forests due to edge effects. The problem of forest fragmentation and subsequent edge effects is especially pressing in Southeast Asia because this region is characterized by the highest relative levels of deforestation and fragmentation in the tropics (Sodhi et al. 2004). Unfortunately, most studies on edge effects have been performed in the Neotropics, with very few examples from Asia (see reviews by Didham & Lawton 1999, Laurance et al. 2002, Broadbent et al. 2008). Asian forests differ substantially in structure and composition from Neotropical forests, with a more open upper canopy and higher density of tall, large diameter trees (Dial et al. 2004, Paoli et al. 2008). Southeast Asian forests in particular also differ in reproductive and seed dispersal behavior, with community-wide mast fruiting events (Appanah 1985, Primack & Corlett 2005) and high frequency of wind dispersal (Gentry 1988; Primack & Corlett 2005).

Previous edge dynamics studies often did not simultaneously examine both sides of the forest edge. In most cases, edge effects on the undisturbed forest side are studied (see reviews by Didham & Lawton 1999, Laurance et al. 2002, Broadbent et al. 2008). Rarely the forest edge in relation to the disturbed vegetation is considered (Gorchov et al. 1993, Cubina & Aide 2001, Dickie et al. 2005, Gunter et al. 2007). However, edge dynamics depend strongly on the interaction between the undisturbed forest and the neighboring disturbed vegetation matrix (Osunkoya 1994, Camargo & Kapos 1995, Newmark 2001, Ries et al. 2004, Cleary & Priadjati 2005, Lawes et al. 2005, Frederiksson et al. 2007, Schedlbauer et al. 2007) and a large fraction of the reported variability in forest edge dynamics can be attributed to differences in disturbance levels of the vegetation matrix (Didham & Lawton 1999, Ries et al. 2004). Furthermore, edge effects work in both directions, i.e., undisturbed forest species colonize the disturbed vegetation while successional or exotic species can invade the undisturbed forest. For a good understanding of forest edge dynamics, it is therefore essential to include both sides of the forest edge.

In this study, we examine the result of 7 yr of forest dynamics along a sharp boundary created by a major fire in 1998 which...
followed a severe drought (Slik & Eichhorn 2003, Cleary & Priadjati 2005, Nieuwstadt & Sheil 2005, Frederiksson et al. 2007, Slik et al. 2008). Our research design incorporated equal representation of burned and unburned forest area, while controlling for topography, slope and fire intensity. We address the following questions: (1) How do these two forest conditions differ in structure, tree species diversity, tree species composition and plant functional traits? (2) Can we detect edge effects and if so, are they biased in one direction or the other, i.e. does the forest interior become more like burned forest or vice versa?

METHODS

FIELD SITE AND PLOT LAYOUT.—The study site (1° 5’ 52.8” S, 116° 49’ 8.4” E) was located in the Sungai Wain Protection Forest near the city of Balikpapan in East Kalimantan Province, Borneo, Indonesia. The area consists mostly of lowland dipterocarp forest typical for eastern lowland Borneo (Slik et al. 2009). The area receives ~2400 mm of rain annually spread equally over the year with rainfall exceeding evaporation in all months. Soils are generally poor and sandy, and the area is characterized by fresh water swamps, river valleys and low hills varying in elevation between 0 and 100 m asl. For a more detailed site description see Nieuwstadt (2002) and Eichhorn (2006). The region was severely hit by the 1997/98 El Nino-Southern Oscillation (ENSO) drought and subsequent fire (Sieger et al. 2001). Although the fires were slow-moving surface fires of low intensity, the damage to the forest understory was catastrophic with mortality rates of near 100 percent for saplings and small trees with a diameter at breast height (dbh) < 10 cm (Slik & Eichhorn 2003, Nieuwstadt & Sheil 2005). Additionally, fire intensity and damage were highly variable, depending on topography, slope and soil moisture content, with some river valleys and swamp areas escaping fire altogether (Slik & Eichhorn 2003). In our research area, the fires were actively extinguished, creating an edge between burned and unburned forest that was created by human activity, instead of any inherent characteristics of the forest that would otherwise complicate interpretation of persistent post-fire differences between burned and unburned forests.

The study was carried out in lowland dipterocarp forest between late 2004 and early 2005, almost 7 yr after the fires that hit the area in April 1998. We chose an area with a relatively straight, North-South oriented unburned–burned forest edge to minimize possible edge shape effects on our study. We made 60 transects of 600 m length perpendicular to the forest edge, with the burned–unburned forest edge located in the middle of each transect. Transects were spaced at 20 m intervals, covering a forest edge length of ca 1300 m. On each transect we established two plots of 10 × 10 m, one in unburned and one in burned forest, both at an equal distance from the forest edge. Distance of the plots from the forest edge along transects was determined randomly (10 m intervals). However, to make sure that each edge distance was represented by an equal number of samples we introduced the constraint that each distance was only allowed to be selected twice. This resulted in the spatial array of plots shown in Figure 1.

PLOT AND TREE MEASUREMENTS.—For each 10 × 10 m plot, we determined elevation, slope, canopy openness, leaf area index (LAI) and fire disturbance. Canopy openness and LAI were determined from hemispherical photographs taken in the center of each plot in a North-South direction at 2 m height. These photographs were analyzed with Winphot software (Steege 1996). Fire disturbance was classified into: (0) no fire disturbance, (1) light fire disturbance if only part of the plot had been burned, (2) medium fire disturbance if the whole plot had burned but most pre-fire poles (trees with dbh between 5 and 10 cm, i.e., large enough not to be recruited after the fire) had survived, (3) heavy fire disturbance if the whole plot had burned with no or few surviving pre-fire poles.

Within each 10 × 10 m plot, we measured the dbh of all trees > 5 cm dbh, including dead standing trees, while all stems taller than 1.3 m and a dbh ≤ 5 cm were measured in a 5 × 5 m subplot that was located in the same corner for each 10 × 10 m plot. All living trees were identified by checking leaf samples against herbarium collections in the Wanariset (WAN, Samboja, East Kalimantan, Indonesia) and Leiden (NHN-L, Leiden University, Leiden, The Netherlands) herbaria. For all species we subsequently measured a suite of functional traits based on at least ten herbarium specimens and the information on their labels in the Leiden herbarium. These traits were: (1) minimum reproductive diameter, determined by ranking the dbh values scored from herbarium labels
of fertile specimens from small to large, plotting them in a scatter-
graph (Y = dbh; X = rank), fitting an exponential function through
the graph, and scoring the Y-intercept of this function as the mini-
umum reproductive dbh; (2) maximum adult diameter, determined
in the same way as minimum reproductive diameter, but this time
with the dbh values ranked from high to low; (3) oven-dry wood
density, based on reported values in the literature (Oey 1990;
Suzuki 1999; Osunkoya et al. 2007), or if no literature values were
available, based on the average wood density of the genus to which
the species belonged because this explains up to 59–70 percent of
species-specific wood density in Indonesian trees (Slik 2006); (4)
leaf shape, defined as blade length divided by blade width; (5) fruit
size, defined as the longest length of the fruit (including wings, if
present); (6) seed size, defined as longest length of the seed (exclud-
ing appendages such as wings or hairs when present); (7) flower size,
defined as maximum flower diameter; (8) dispersal mode, either
animal (fruits/seeds with edible parts and/or bright colors), gravity
(fruits/seeds with no visible animal or wind dispersal adapted struc-
tures) or wind (fruits/seeds with wings, long hairs or broad flattened
appendages). These characters were selected because they provide
important information on tree life-history strategies, especially in
relation to tree species successional status (Westoby et al. 2002,
2006, Wright et al. 2007).

DATA PREPARATION.—We subdivided our stem data in three diam-
ter classes to compare differences between tree regeneration classes:
(1) saplings, height taller than 1.3 m and dbh ≤ 5 cm; (2) poles,
dbh 5.1–10 cm; and (3) trees, dbh > 10 cm. Preliminary analysis of
stem density and basal area in each 10 × 10 m plot showed that
many burned forest plots contained very few stems, making it dif-
cult to compare diversity, composition and functional traits among
plots directly. To overcome this we based our analysis on equal
numbers of stems, not area, by sorting all stems according to their
distance along the 600 m transect lengths. We then selected groups
of 20 stems, without replacement, going from 0 to 600 m along the
unburned–burned forest gradient. This procedure was repeated for
each of the three tree diameter classes. While this solves the problem
of low and unequal plot stem densities, it introduces unequal vari-
cance in transect length covered per sample in unburned vs. burned
forest because stem densities differed between these forest types.
This could result in more β-diversity included in burned than in
unburned forest samples, and might thus slightly over-estimate
diversity in burned forest while under-estimating compositional
differences between unburned and burned forest. However, these
biases are limited compared with those introduced by the alterna-
tive method of using equal area comparisons (plots) with variable
stem numbers.

For each 20 stem sample we determined basal area and species
based averages of minimum reproductive diameter, maximum
adult diameter, oven-dry wood density, leaf shape, fruit size, seed
size, and flower size. Additionally, we determined percentage of
wind- and gravity- and animal-dispersed species. Except for basal area,
which was calculated using all 20 stems in each sample, the other
traits were calculated using species averages to avoid biases caused
by very abundant species. Sample stem density, slope, elevation,
canopy openness, LAI, distance from forest edge and fire intensity
were determined by assigning each stem the value of the plot where
it was found and then calculating the average value for these
parameters based on the 20 stems in each sample.

Species compositional values for each sample of 20 stems were
based on detrended correspondence analysis (DCA), using the
samples as cases and the species presence/absence as variables. We
combined the samples of all diameter classes in one analysis to
make compositional values comparable between diameter classes.
The analysis revealed that the first DCA-axis corresponded strongly
with disturbance with a clear separation between burned and
unburned forest samples. Therefore, we compared compositional
differences between samples using their loading on the first
DCA-axis.

DETECTING DIFFERENCES BETWEEN UNBURNED AND BURNED FOREST.—
We compared all variables between unburned and burned forests
using the nonparametric Mann–Whitney test. Nonparametric test-
ing was used because data variance levels between unburned and
burned forests were usually significantly different and could not be
corrected by standard data transformations.

EDGE EFFECT ANALYSIS.—Since edge effects can be confounded by
variation in elevation, slopes and especially fire intensity we applied
partial correlation analysis to detect significant correlations between
distance from the forest edge and the study variables. Partial corre-
lation produces correlation coefficients that have been corrected for
covariation of other variables included in the analysis, i.e., any
confounding effect of elevation, slope and fire intensity on the cor-
relation coefficient between the study variable and distance from
the forest edge is controlled for by this type of analysis. We per-
formed the partial correlation using both the original edge distance
data and the log transformed edge distance data to test for linear
and nonlinear (logarithmic) relationships with the test variables,
respectively.

RESULTS

UNBURNED–BURNED FOREST COMPARISONS.—Almost 7 yr after fire
we still detected highly significant differences between unburned
and burned forest in most measured variables (Figs. 2, 3 and 4) and
many either increased or declined with increasing diameter class. Of
the forest structural variables (Fig. 2) differences between burned
and unburned forest with increasing diameter class declined for
stem density and basal area, remained constant for canopy openness
and increased for LAI and the number of dead standing trees. Tree
diversity, composition and dispersal strategies mostly showed in-
creasing differences between burned and unburned forest with in-
creasing diameter class (Fig. 3). Functional traits (Fig. 4) show
increasing differences between burned and unburned forest with
diameter class for wood density, seed size, leaf shape and reproduc-
tive dbh, while no change was detected for flower size and a decline
for maximum dbh and fruit size.
Composition and abundances of the top ten most common species in each diameter class differed dramatically between unburned and burned forest (Table 1). Only a few of the top ten abundant species in unburned forest were still found among the top ten common species in burned forest, while many of the top ten species in burned forest were very rare or absent in the unburned forest plots. Notably, differences in diversity and composition, together with pioneer species dominance, were lowest in the smallest diameter class.

**EDGE EFFECTS.**—We only detected a few significant edge effects (Table 2): a decreasing LAI away from the forest edge in burned

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FIGURE 2. Comparison of the medians of several forest structural variables between burned and unburned forest as measured for three tree size classes. Significance levels indicated with stars (*0.05 < P > 0.01; **0.01 < P > 0.001; ***P < 0.001).
forest; an increasing number and basal area of saplings away from the forest edge in unburned forest; an increasing number of dead standing saplings away from the forest edge in both burned and unburned forest; declining numbers of dead standing poles and trees away from the forest edge in unburned forest; increasing sapling diversity away from the forest edge in burned forest; a shift in sapling species diversity.
FIGURE 4. Comparison of the medians of several species functional traits between burned and unburned forest as measured for three tree size classes. Significance levels indicated with stars (*0.05 < P > 0.01; **0.01 < P > 0.001; ***P < 0.001).
| TABLE 1. The ten most abundant species in number per ha and percentage of stems per diameter class in unburned and bordering burned forest, 7 yr after fire. Top ten species in unburned forest are indicated in bold in the burned forest. Species authors can be found at (http://www.asianplant.net). |
|---|---|---|---|---|---|---|---|---|---|---|
| | Unburned (0–5.0 cm) | N (ha) | N (%) | Unburned (5.1–10.0 cm) | N (ha) | N (%) | Unburned (> 10.0 cm) | N (ha) | N (%) |
| **Shorea laevis** | 766.7 | 7.8 | **M. lowii** | 98.3 | 10.4 | **M. lowii** | 30.0 | 6.3 |
| **Macaranga lowii** | 500.0 | 5.1 | **Madhuca kingiana** | 56.7 | 6.0 | **G. nervosa** | 20.0 | 4.2 |
| **Gironniera nervosa** | 366.7 | 3.7 | **D. acutifolius** | 26.7 | 2.8 | **M. kingiana** | 16.7 | 3.5 |
| **Urophyllum arboreum** | 300.0 | 3.1 | **Aporusa subcutata** | 25.0 | 2.6 | **S. laevis** | 16.7 | 3.5 |
| **Fordia splendidissima** | 286.7 | 2.9 | **Cleistanthus erycibifolius** | 25.0 | 2.6 | **D. acutifolius** | 15.0 | 3.1 |
| **Dipterocarpus confertus** | 213.3 | 2.2 | **S. laevis** | 23.3 | 2.5 | **Papaya lucida** | 13.3 | 2.8 |
| **Dario acutifolius** | 200.0 | 2.0 | **G. nervosa** | 21.7 | 2.3 | **D. confertus** | 11.7 | 2.4 |
| **Melanocarpa fulcinervis** | 186.7 | 1.9 | **D. confertus** | 16.7 | 1.8 | **Syzygium tawabense** | 11.7 | 2.4 |
| **Vatica umbonata** | 186.7 | 1.9 | **Dacrydium rostrata** | 15.0 | 1.6 | **D. kikir** | 10.0 | 2.1 |
| **Syzygium laxiflorum** | 180.0 | 1.8 | **Drypetes kikir** | 13.3 | 1.4 | **V. umbonata** | 8.3 | 1.7 |
| **Burned (0–5.0 cm) | N (ha) | N (%) | Burned (5.1–10.0 cm) | N (ha) | N (%) | Burned (> 10.0 cm) | N (ha) | N (%) |
| **Pterandra coerulescens** | 206.7 | 7.0 | **Macaranga gigantea** | 140.0 | 22.8 | **M. gigantea** | 215.0 | 47.7 |
| **Dillenia grandifolia** | 146.7 | 5.0 | **V. arborea** | 71.7 | 11.7 | **V. arborea** | 70.0 | 15.6 |
| **F. splendidissima** | 140.0 | 4.8 | **D. grandifolia** | 26.7 | 4.3 | **M. kingiana** | 10.0 | 2.2 |
| **M. lowii** | 93.3 | 3.2 | **D. confertus** | 16.7 | 2.7 | **E. diadenum** | 6.7 | 1.5 |
| **U. arboreum** | 93.3 | 3.2 | **Macaranga bancana** | 15.0 | 2.4 | **D. confertus** | 5.0 | 1.1 |
| **Anthocephalus chinensis** | 86.7 | 3.0 | **P. coeruleus** | 13.3 | 2.2 | **Knema palkens** | 5.0 | 1.1 |
| **Crudia reticulata** | 86.7 | 3.0 | **Barringtonia macrotheca** | 11.7 | 1.9 | **M. bancana** | 5.0 | 1.1 |
| **Vernonia arborea** | 86.7 | 3.0 | **Ficus aurata** | 11.7 | 1.9 | **Chetionarpus ascaris** | 3.3 | 0.7 |
| **G. nervosa** | 66.7 | 2.3 | **Enopogonum diadenum** | 10.0 | 1.6 | **Cassogylum sumatrana** | 3.3 | 0.7 |
| **Glochidion glomeratum** | 66.7 | 2.3 | **M. kingiana** | 10.0 | 1.6 | **D. acutifolius** | 3.3 | 0.7 |

*Species authors can be found at (http://www.asianplant.net).*
composition toward the forest edge in unburned forest; declining percentage of animal-dispersed poles away from the forest edge in unburned forest; and declining percentage of gravity-dispersed trees away from the forest edge in burned forest. Of the functional traits only reproductive dbh showed a significant edge effect for poles in unburned forest.

**DISCUSSION**

The lasting impact of fire.—We observed large and significant differences between unburned and burned forest in almost all measured variables 7 yr after fire. This is not surprising given the huge impact that the fires had on the forest ecosystem in our study area, resulting in overall tree mortality rates of ~70 percent, and almost 100 percent mortality for trees with a diameter <10 cm shortly after the 1998 fires (Slik & Eichhorn 2003, Cleary & Priadjati 2005, Nieuwstadt & Sheil 2005, Slik et al. 2002). Despite the fact that stem densities and basal areas of trees (dbh >10 cm) were comparable between the two forest conditions, the burned forest canopy remained underdeveloped, as indicated by greater canopy openness and lower LAI. This was mainly caused by the low density and basal area of understory vegetation and the dominance of a few fast growing pioneer species that had already reached the canopy since the 1998 fires. These species were generally characterized by relatively large, rounded leaves placed terminally on the branches producing a wide but shallow crown, creating a relatively open and single-layered canopy.

The dominance of pioneer species in burned forest was also reflected in the large difference in species composition with unburned forest, even though species diversity among saplings and poles (dbh <10 cm) did not differ. The lower stem densities in the small diameter classes (dbh <10 cm) together with the large compositional difference with unburned forest indicate that regeneration toward an old growth forest species composition in the burned forest is slow, confirming similar long-term observations from burned forests around the tropics (Riswan et al. 1985, Slik et al. 2002, Chazdon 2003, Cochrane 2003, Barlow & Peres 2008). However, the smaller compositional difference between burned and unburned forest in the smallest diameter class, as compared with the larger diameter classes, indicates an increasing dominance of old growth forest species. This apparent recovery, however, is most likely caused by the fact that the pioneer trees started to grow into the larger diameter classes while the slower growing old growth species that had survived the fire remained behind in the smallest diameter class.

The strong shift toward an early successional vegetation type in burned forest was also clear from the pronounced difference in tree species functional traits compared with unburned forest. Trees in the burned forest were characterized by lower wood densities, indicative of fast growth rates (King et al. 2005), which together with the relatively small maximum stature and small reproductive diameter suggest reproductive maturity at an early age. Contrasting with the narrow leaves found in the unburned forest, the burned forest was dominated by species with more rounded leaves, indicating higher photosynthetic capacity (Popma et al. 1992, Westoby et al. 2002, Falster & Westoby 2003). Also, fruit and seed sizes were smaller in burned forest, indicating lower shade tolerance.
(Osunkoya et al. 1994, Coomes & Grubb 2003, Slik 2005), higher fruit and seed production, combined with better colonizing ability (Hammond & Brown 1995, Westoby et al. 2002, Coomes & Grubb 2003) compared with the species in unburned forest. Many of the newly established and now dominant tree species in the burned forest also produced seeds capable of dormancy, meaning that they can, unlike most species in the unburned forest, survive in the soil seed bank (Ng 1980, Nieuwstadt 2002).

**Impact of Neighboring Old Growth Forest on Burned Forest Regeneration.**—Very few variables showed a correlation with distance from forest edge in burned forest. This emphasizes the importance of local processes such as stump or root sprouting, seed rain from locally surviving adult trees, and germination from the soil seed bank for the initial regeneration of the old growth forest species in burned forests and agrees with other studies that indicate very limited impact of and species exchange between undisturbed and bordering disturbed forest (Osunkoya et al. 1994, Ries et al. 2004, Lawes et al. 2005, Schedlbauer et al. 2007). However, it contradicts general ideas about the importance of proximity of old growth forests for secondary forest compositional recovery (Chazdon et al. 2009), and observations on the importance of remnant trees and vegetation for seed dispersal from undisturbed into disturbed vegetations (Zahawi & Augspurger 2006). In this case a possible explanation for this discrepancy might be related to the mast fruiting strategy of most late successional tree species in Asian forests, i.e., trees fruit synchronously but irregularly at intervals of several years (Appanah 1985, Primack & Corlett 2005). No large mast fruiting event was recorded for our study site and Borneo in general between 1998 and 2005 (G. M. Frederiksson, pers. comm., and comments posted on Mastwatch: http://www.phylodiversity.net/mastwatch/), meaning that seed rain from the undisturbed forest into the burned forest has been limited.

More generally valid explanations across the tropics might be related to adverse seedling establishment conditions in burned forests for old growth forest tree species. The dominating early successional species usually produce a thick litter layer consisting mainly of large leaves which can inhibit establishment of seedlings (Molofsky & Augspurger 1992). Even if young seedlings manage to reach the soil they will find that the mycorrhizal fungi community differs between undisturbed and disturbed forest (Dickie et al. 2005) providing unsuitable establishment conditions for some species. Also, several studies have found that seed predator and herbivore densities differ between undisturbed and disturbed forests, especially near the forest edge (Osunkoya et al. 1994, Galetti et al. 2003). Successful re-establishment of pre-fire species will therefore be a slow process that depends not only on seed input of old growth species, but also on processes related to litter dynamics, plant–herbivore interactions, seed predation levels and soils. However, we like to emphasize that some recovery was already taking place in the burned forest, as was indicated by the nonexistent difference in diversity and reduced compositional difference in the smallest diameter class compared with adjacent unburned forest. Our results indicate that this recovery is currently more driven by processes in the burned forest itself than by colonization from the unburned forest.

**Impact of Burned Forest on Old Growth Forest Integrity.**—Our data indicates that the forest edge has very limited impact on light conditions, tree diversity, functional traits and species composition in unburned forest, contrasting sharply with studies from the Neotropics (Laurance et al. 2002). The limited impact of light and micro-climate related edge effects on old growth forest in our study is probably related to the fact that the most adverse edge effects were reduced by the development of a closed canopy of considerable height (15–20 m) in the bordering secondary forest within 7 yr. Furthermore, Bornean old growth forests are characterized by a relatively tall, but open canopy structure, possibly making them more resilient to edge effects than their Neotropical counterparts.

Although edge effects were limited in the undisturbed forest, we did observe some edge effects, such as decreasing numbers of dead standing saplings (dbh ≤ 5 cm) toward the forest edge, a pattern that was also observed in the burned forest. In the case of the unburned forest the decline in dead standing saplings was accompanied by a decline in live sapling density toward the forest edge. This suggests higher sapling survival accompanied by lowered sapling recruitment rates near the forest edge. This pattern of lowered recruitment might be explained by hampered seed input, i.e., seed input of old growth forest species can only arrive from one direction, the forest interior, as opposed to sites further from the forest edge that may receive seeds from all directions. Indeed, seed rain has been shown to be less diverse, especially for large seeds, in forest edges (Lopes de Melo et al. 2006).

The reduced mortality for saplings was opposite to the pattern observed for larger diameter trees (dbh > 5 cm) which showed increasing mortality toward the forest edge, corresponding to results from other studies that report increased tree mortality up to 1200 m from the forest edge (Laurance et al. 2001a, b; D’Angelo et al. 2004; Frederiksson et al. 2007). This increased tree mortality has been linked to increased wind disturbance, causing more tree falls near the forest edge. In our study area it is more likely that the tree mortality is caused by increased drought susceptibility near the forest edge, with higher insolation, more wind and lower air humidity, especially during infrequent but severe ENSO-associated droughts that occur in eastern Borneo (Laurance et al. 2001a, b, Nieuwstadt & Sheil 2005). This is in accordance with the high tree mortality observed in the more exposed burned forest. Earlier studies have already shown that drought especially affects large trees during severe droughts (Slik & Eichhorn 2003, Nieuwstadt & Sheil 2005).

Another noticeable long distance edge effect in unburned forest concerned the increasing percentage of animal dispersed tree species in the 5.1–10 cm diam class. As most of these trees were already established before the 1998 fire, this change may result from selective mortality of gravity and wind dispersed plant groups near the forest edge rather than an increase in animal dispersed trees. Many gravity dispersed trees are extremely shade-tolerant understory to sub-canopy species and are susceptible to the microclimatic changes associated with edge effects (Benitez-Malvido & Lemus-Albor 2005). Also, wind dispersal is a typical dispersal strategy of old growth forest trees (e.g., Dipterocarpaceae) in Borneo (Primack & Corlett 2005), unlike most other tropical regions where it is usually associated with a pioneer strategy.
CONCLUSIONS

Our results show that forest fires in Asian tropical rain forests have a lasting impact on forest structure and tree species composition, with very limited exchange of late successional species from the undisturbed to the neighboring burned forest during the first few years of regeneration. This might be a common pattern in Asian tropical rain forests which are characterized by mast fruiting, meaning that seed input from undisturbed forest into disturbed forest is irregular and can be completely lacking for many years. Other studies have shown that this lack of recovery or even deterioration in species composition and forest structure can last at least 20 yr (Slik et al. 2002, Barlow & Peres 2008, Slik et al. 2008). However, there is also a lot of evidence showing that almost all old growth tropical forests around the world are affected by rare fire events (Power et al. 2008), from which they apparently recovered. Our own data suggests that compositional recovery was already happening in the smallest diameter class, although this recovery is most likely not driven by colonization from the neighboring undisturbed forest but by growth of pioneer species into the larger diameter classes thus leaving the slower growing climax species that survived the fire in the burned forest understory. Therefore it is extremely important to maintain strict protection for burned forests so that the in situ regeneration process is not disturbed. Since most climax tree species were still present in the burned forest, these forests have the potential for full recovery and actions to prevent further fires, such as creation of fire breaks, should be considered as a management option.

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LITERATURE CITED


