

SECONDARY FOREST SUCCESSION OF RAINFORESTS IN EAST KALIMANTAN: A PRELIMINARY DATA ANALYSIS

René Verburg, Ferry Slik, Gerrit Heil, Marco Roos and Pieter Baas

SUMMARY

Today, large areas of primary rainforest in Kalimantan have been converted into secondary forests. The state of secondary forests is not permanent, because forests may recover from disturbance through secondary succession. Vegetation structure and species composition after disturbance may differ widely among secondary forests, depending on disturbance type, the time elapsed since disturbance and local site conditions. Because of this, it becomes very difficult to predict the effects of disturbance on future changes in species composition.

During secondary succession, species composition will change in such way that, in forests disturbed recently, only the composition of small trees will deviate from that of virgin forests while, in forests disturbed longer ago, the composition of the larger trees will have changed. To test whether succession in secondary forests can be studied using such a size-structured analysis, we applied a Detrended Correspondence Analysis (DCA) to a forest inventory database. This database contained information on the diameter measurements of tree species ≥ 10 cm DBH. In forests that were burnt 1 year ago we found relatively small shifts in species composition for small trees (trees with a diameter of 10-20 cm DBH). The largest deviation in species composition was found for trees with a diameter of 30 cm DBH or more. Thus forest fires have a large impact on the composition of canopy and emergent trees species. Logging affected species composition in two ways. As expected, one year after logging, a shift in species composition was found for trees having a diameter of 50 cm and more (these are the timber trees). Unexpectedly, this compositional shift becomes even larger in forests that were logged 15 years and 25 years ago. Thus logging can have a significant effect on the future composition of canopy and emergent tree species (the future timber species), as compared to the species composition in primary forest. Moreover, a large compositional shift was also found for trees with a diameter of between 10 and 30 cm DBH. This shift is mainly caused by a larger in-growth of small (trees with a diameter < 10 cm) understorey tree species. We could not detect a significant increase in the number of pioneer species for these stem diameter classes (10-30 cm DBH) in logged forests as compared to primary forest.

This preliminary analysis was carried out on only 6 plots, each having a sample area of 1.5 ha. In order to generalise these results we should also analyse species composition in plots from different regions in Kalimantan. However, species composition is also likely to be site-specific, because of the occurrence of regional patterns in species distribution. A better way of generalising patterns in compositional changes of species assemblages caused by disturbance might be to assign species to plant functional types. To do this would require additional information on tree characteristics such as wood density and seed size. After species have been assigned to groups, shifts in abundance of plant functional types as a response to disturbance can be modelled.

INTRODUCTION

Vast areas of primary rainforest in Kalimantan (Indonesia) today are being lost through exploitation, large-scale fires and conversion to agriculture. As a result, degraded vegetation types and secondary forests are replacing patches of species-rich lowland rainforest. Most countries in the tropics, including Indonesia, now carry equal or larger areas of secondary forests than of original primary forest (*e.g.*, Brown and Lugo, 1990). It is therefore becoming increasingly important not only to protect and conserve patches of remaining primary forest, but also to investigate the possibilities of recovering the original biodiversity levels of secondary forests.

In late successional forests, small-scale disturbance, caused by tree fall, provides gaps in which early successional species (*i.e.*, pioneer species) can fulfil their growth cycle. In addition, landslides and erosion may cause natural large-scale disturbance (*e.g.*, Richards, 1996; Whitmore, 1989, 1991). Disturbance caused by human interference varies widely in scale, type and intensity. Such disturbance can range from gap formation caused by reduced impact logging to large-scale and repetitive slash and burn activities. Because type and intensity of disturbance varies, an array of degraded vegetation types follows, varying in structure and species diversity (*e.g.*, Finegan, 1996). Disturbed vegetation types are not static, so they may recover from disturbance (Brown and Lugo, 1990; Riswan and Kartawinata, 1991; Whitmore, 1991; Terborgh and Petren, 1991; Finegan, 1996; Miller and Kauffman, 1998). For example, reduced impact logging may cause only localised damage and result in gap formation (*e.g.*, Whitmore, 1991). If the gaps are not too large, forest patches can quickly regenerate through secondary succession and the original vegetation can recover. At the other extreme, fire, clear cutting, and shifting cultivation (*e.g.*, slash and burn activities) usually result in much larger areas of degraded vegetation. When, in addition, disturbance is frequent, through continued human interference, the vegetation will consist solely of *Imperata* grasses (*e.g.*, MacKinnon *et al.*, 1996; Richards, 1996). Such vegetation might also recover from disturbance, but only after human pressure has ceased and after a long period of time (MacKinnon *et al.*, 1996; Finegan, 1996).

A unique feature of lowland climax rainforest of Southeast Asia is that a single plant family, notably the Dipterocarpaceae family, accounts for many of the large trees (emergents), and hence this lowland rainforest is called Mixed Dipterocarp Forest (MDF) (*e.g.*, Whitmore, 1989, 1991; Schulte and Schöne, 1996; Richards, 1996). As in all tropical lowland rainforests of the world, total species richness in MDF is high. Whitmore (1989, 1991) reported, between 150 and 175 different tree species per hectare amongst trees of ≥ 10 cm DBH. Secondary forests, on the other hand, have fewer species. This is partly from the result of environmental conditions in secondary forests which promote growth of early successional pioneers, of which there are fewer species (Richards, 1996; Whitmore, 1989, 1991).

Species diversity in secondary forests may increase as the forest patches develop, so that eventually the high species diversity of late successional MDF can be reached. The question then arises of whether predictions can be made from forest inventories about the development of species diversity from disturbed secondary forest patches to late successional forest.

AN EXAMPLE OF THE DATA ANALYSIS

A number of forest inventory databases are available for analysis within the MOFEC-Tropenbos programme. These databases contain species lists and tree diameter measurements (DBH) only. If model predictions are to be made on the shifts in species composition caused by disturbance, we need first to analyse the underlying processes causing these shifts. After disturbance, gaps are created where large old trees have disappeared and in which new trees can invade. The higher light levels created by gaps may cause increased growth rates for understorey tree species, as well as more favourable germination conditions for the seeds of pioneer species. The recovery of a forest patch is driven by secondary succession. Succession is the process of 'species turnover', which leads to changes in vegetation cover and type (*e.g.*, Usher, 1992, see Figure 1).

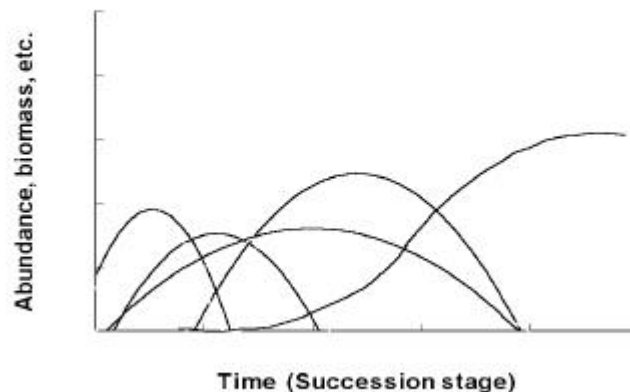


Figure 1 A hypothetical sequence of a number of species, species groups, guilds or plant functional types (PFT) during succession. (*e.g.*, Usher, 1992).

In the case of secondary forest succession, do tree species already present in the forest 'reclaim' the gap created by disturbance or do we find new species? As the new stand develops, species composition may further deviate from the original species association. Sheil (1999) introduced a method for analysing some temporal aspects of succession. The rationale behind this method is that big stems reflect the past composition of small stems (Sheil, 1999). Using this size-structured analysis, we studied the changes in species composition of trees belonging to various stem diameter classes. Sheil (1999) used a multivariate technique called Detrended Correspondence Analysis (DCA, *e.g.*, Hill and Gauch, 1980; ter Braak, 1985). In short, a Correspondence Analysis comprises an Eigen analysis, in which a similarity matrix of cases (plots) and variables is produced, based on chi-square distances, by the column and row totals of the matrix. Plots are arranged along the axes according to the variation explained in the data. Thus axis 1 explains the largest variation and subsequent axes residual variation. A Detrended CA is different in that it corrects for a major defect of ordination methods called the 'Arch' or *e.g.*, Hill and Gauch, 1980; ter Braak, 1985). Sheil (1999) was able to arrange plots along the first DCA axis according to their 'successional status', and showed that

species composition in early successional forest largely differed from late successional forest depending on the stem diameter of the trees analysed. This difference depends on the time that has elapsed since disturbance, the speed of succession, growth of pioneer trees and local growing conditions.

We examined the species composition of different primary and secondary forests from a large forest inventory database containing information on tree species abundance and diameter measurements of trees from different localities in East Kalimantan. For the analysis shown here we used data from one locality only. A detailed site description of this locality can be found in Slik *et al.* (in prep.). The inventory concerned was carried out in the International Timber Corporation Indonesia (ITCI) concession (see Table 1).

Table 1 The 6 plots in the ITCI concession. IT-1 is primary forest, while IT-2 through IT-6 are plots in disturbed secondary forests. The location, total sampled area (in hectares), species diversity (Fishers α , Fisher *et al.*, 1943, Taylor *et al.*, 1976), number of stems (trees ≥ 10 cm DBH) and number of tree species (stems ≥ 10 cm DBH) are given for each plot.

Plot	Type	Location	Area	Fishers α	Stems	Species
IT-1	Primary forest	116°26' E; 0°52' S	1.5	96.1	523	179
IT-2	Logged 1 year ago	116°21' E; 0°52' S	1.5	68.8	325	120
IT-3	Logged 15 years ago	116°31' E; 0°55' S	1.5	105.6	596	200
IT-4	Logged 25 years ago	116°35' E; 0°53' S	1.5	98.3	581	190
IT-5	Primary forest, burnt 1 year ago	116°27' E; 0°48' S	1.5	65.5	376	125
IT-6	Logged 15 years ago, burnt 1 year ago	116°30' E; 0°51' S	1.5	94.0	411	158

Five replicate plots (each 30 x 100 m) were laid out for each forest type (primary forest and secondary forests disturbed by logging and by fire), giving a total sampling area of 1.5 hectare per forest type (table 1). For the logged plots, logging intensities varied around 10 trees per ha (MacKinnon *et al.*, 1996). All trees ≥ 10 cm DBH were identified in each forest type and their diameters measured. To study the recovery of the vegetation and thus changes in species composition as affected by disturbance, we analysed species composition in different forests per stem diameter class. Stem diameter classes were assigned per 10 cm interval, starting from 10 cm DBH. The largest diameter class comprised stems of 60 cm DBH and larger. We expected that species composition in logged plots would differ largely from primary forest for small diameter classes. This difference would be smaller in the 25 year-old logged forest than in the 15 year-old logged forest, because species composition in 25 year-old logged forest would gradually converge to that typically found in primary forest. We could not test the same hypothesis for secondary forests disturbed by fire, since we had data only for secondary forests disturbed by fires one year ago. We therefore analysed only species-specific mortality patterns caused by fire for different stem diameter classes.

We expected plots to be ordered according to disturbance history and type. For the ordination we used stem counts per species. Species for some genera could not be identified. These individuals were grouped per genus. Typical ordination patterns are shown in Figure 2 for stem diameter classes 10-20 cm and for class ≥ 60 cm DBH. We interpreted plot position along axis I of the DCA as a 'successional score' (*i.e.*, Sheil, 1999). An ordination was performed for each

stem diameter class and Figure 3 shows the axis I scores of plots for all stem diameter classes. The effects of fire on the mortality of tree species for different stem diameter classes can be studied by comparing plots IT-5 (primary forest disturbed by fire) with IT-1 (primary forest), and plots IT-6 (secondary forest logged 15 years ago and disturbed by fire) with IT-3 (forest logged 15 years ago). For both primary and logged forest, the effect of fire on species composition is relatively small for trees in diameter class 10-20 cm DBH, but much larger for trees in class 20-30 cm DBH. The largest differences were found in stem diameter classes 30-40 and 40-50 cm DBH, which include understorey and sub-canopy trees (Figure 3). For class 30-40 cm DBH, this difference was much larger for primary forest disturbed by fire than for logged forest disturbed by fire.

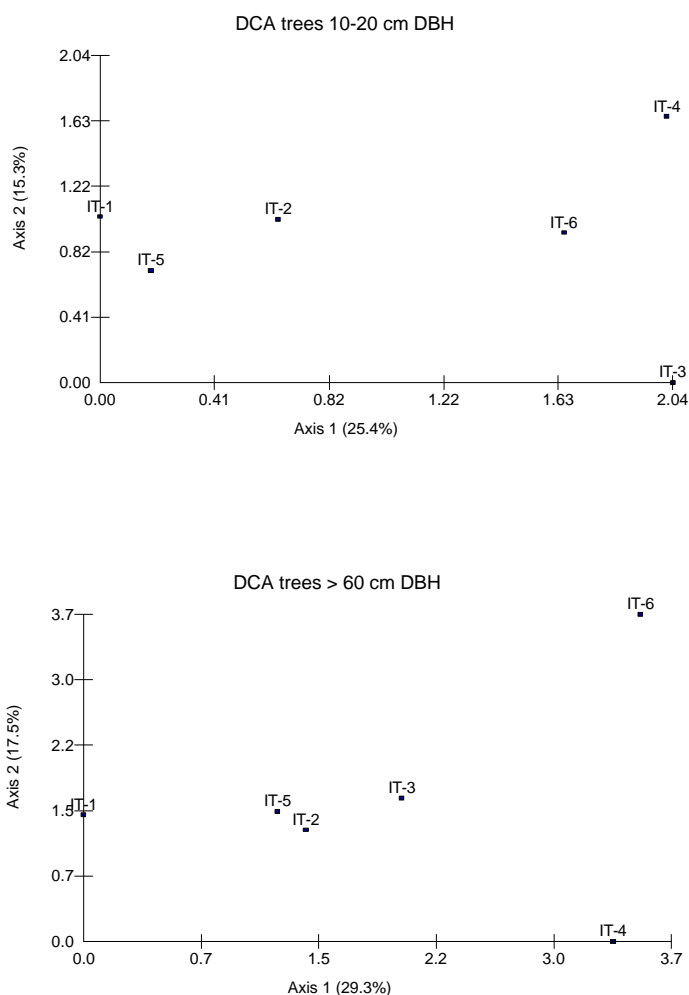


Figure 2 Detrended Correspondence Analysis of plots from the ITCI concession for stems between 10 and 20 cm DBH (top) and for stems \geq 60 cm DBH (bottom). Only the first two axes are shown for both graphs. For explanation of plot codes (IT-1 to IT-6) see Table 1.

Among the logged plots, we expected that plot IT-2 (logged 1 year ago) would show the smallest deviation from primary forest for all stem diameter classes. Plot IT-2 did indeed have the most comparable species composition with primary forest among the logged plots, but the compositional shift from primary forest was greater for large diameter classes (50-60 and ≥ 60 cm DBH). This may be the result of the selective removal of timber trees belonging to these diameter classes. We found two large compositional shifts in the logged plots IT-3 and IT-4 (15 years and 25 years after logging, respectively). The largest deviations from primary forest were found for diameter classes 10-20 cm and 20-30 cm, and for diameter classes 50-60 cm and ≥ 60 cm DBH. Thus logging caused a compositional shift from primary forest for understorey, canopy and emergent trees, while the larger understorey and sub-canopy tree composition showed little change. Because this shift becomes even larger in plot IT-4 (logged 25 years ago), we expect logging to have a large temporal effect on the future species composition of large canopy and emergent species.

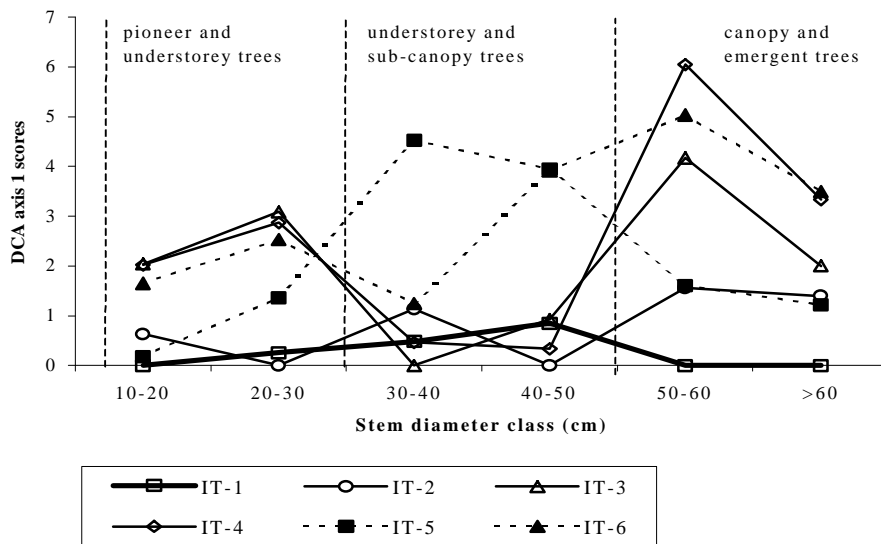


Figure 3 The position of plots from the ITCI concession along the first axis of the Detrended Correspondence Analysis for each stem diameter class. For explanation of plot codes (IT-1 to IT-6) see Table 1. Black symbols connected with dashed lines include fire-affected plots, open squares connected with thick lines primary forest and open circles, triangles, and diamonds connected with lines include logged forests.

Pioneer species like *Macaranga pearsonii* and *M. gigantea* can grow up to an average DBH of 21 and 28 cm, respectively, in 25 years (Slik, pers. obs.). We expected to find a larger number of pioneer species in diameter classes 10-20 and 20-30 cm DBH in logged forest as compared with primary forest. However, for diameter classes 10-20 and 20-30 cm DBH, we did not find a significant difference in the number of pioneer trees between the logged plots and the primary forest plot (Table 2). Thus this compositional shift in logged forests may be due to a stronger in-growth of understorey tree species rather than a larger invasion of pioneer species. These small understorey trees could well be future sub-canopy, canopy or emergent species.

Table 2 The number of pioneer and non-pioneer species (as % of the total number of tree species) for stem diameter classes 10-20 and 20-30 cm DBH for the plots in primary (IT-1), 2 year-old logged (IT-2), 15 year-old logged (IT-3), and 25 year-old logged forest. Pioneers include all species defined as 'species found in secondary forests' (Keßler and Sidiyasa, 1994). Distribution of pioneer and non-pioneer species in different logged plots did not differ significantly from the distribution in primary forest (Chi-square test with Bonferoni correction for multiple comparisons).

Plot	10-20 cm		20-30 cm	
	Pioneers	Non-pioneers	Pioneers	Non-pioneers
IT-1	27	73	17	83
IT-2	25	75	20	80
IT-3	29	71	31	69
IT-4	33	67	25	75

MODELLING SECONDARY FOREST SUCCESSION

Although our preliminary results on the species compositional shifts due to disturbance seem straightforward, it should be noted that it is difficult to generalise from these results, since we analysed only 6 plots at one locality. In a first database survey we carried out a DCA in which plots from different regions of East Kalimantan were put into one ordination (data not shown). We expected plots of disturbed forests to have a similar ranking to that shown in Figure 3, while regional differences in species composition could affect the plot ranking along subsequent axes. However, regional differences in species composition affected plot ranking along the first three axes of the DCA. This implies that an analysis of species composition as affected by disturbance may only be analysed per floristic region, because species assemblage may differ widely between different regions. Indeed, types can differ considerably among secondary forest vegetation, depending on local site conditions as well as on disturbance type (*e.g.*, Laumonier, 1997). This may have significantly affect the modelling of secondary succession based on changes in species composition only.

Simulation models have proved to be useful tools for predicting the effects of large-scale disturbance on both ecosystems and their recovery (*e.g.*, Heil and Bobbink, 1993; van Deursen and Heil, 1993; Moilanen and Hanski, 1995; Deutschman *et al.*, 1997). One way to understand the process of secondary forest succession is to develop a simulation model, because this forces us to formalise ecological processes and therefore increases our understanding of how disturbance acts on the functioning of ecosystems. Moreover, simulation models also provide results which can support policy making, such as in land-use planning.

In modelling secondary forest succession, we should look at changes in the functional aspects of the forest rather than to try to model changes in species lists. For the purposes of this model, species are usually assigned into different plant functional types (PFT, *e.g.*, Condit *et al.*, 1996; Lavorel *et al.*, 1997). Classifying tree species into different functional types requires additional information on tree characteristics and life history parameters. Information such as growth and mortality rates, wood density and seed size can be used as proxy parameters for species assemblages in a model. Unfortunately, such information for tree species from Kalimantan is rare and, where it is available, rather scattered through the literature (but see Raich and Gong,

1990; Suzuki, 1999). We are currently carrying out both a literature survey and additional measurements on such plant parameters to add to the species lists.

A number of model types are now available which deal with the simulation of forest succession (West *et al.*, 1981; Bossel, 1991; Huston, 1992; van Hulst, 1992; Usher, 1992; Bossel and Krieger, 1994; Köhler and Huth, 1998; Givnish, 1999). Moreover, within the last few years, these models have become based more on individual trees - (*e.g.*, Bossel, 1991; Huston, 1992; Urban and Shugart, 1992; Bossel and Krieger, 1994; Köhler and Huth, 1998; Chave, 1999). In our study, we may treat different plant functional types as individual trees and model changes in abundance of PFTs as affected by disturbance. A next step is to develop the model in such a way that changes in species groups (PFTs) as affected by disturbance and regrowth are extrapolated to a larger spatial scale (*i.e.*, at a landscape level). This requires information on habitat distribution and patchiness (*i.e.*, habitat fragmentation) over a landscape, since the possibility and speed of recovery of disturbed forests depends on the presence of nearby forest patches to serve as sources for new trees. This information can be derived from Remote Sensing (RS) satellite images. Changes in fragmentation of forest patches through time can be analysed from RS images and may give land-use planners information on the possibilities for recovery of secondary forests.

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