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Assessing tropical lowland forest disturbance using plant morphological and ecological attributes

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Abstract

Secondary forests now play a vital role in the conservation of tree species diversity in Southeast Asia because of the continuing fragmentation and decreasing extent of undisturbed forests in this region. To be able to determine the structural and compositional integrity of secondary forests, a ground based rapid assessment method was developed. For this purpose species from the genera *Macaranga* and *Mallotus* (Euphorbiaceae) were classified into early and late successional species based on morphological characters that were found to correlate with the light establishment preferences of these species. These characters were wood density (found to be significantly negatively correlated with light establishment preference), seed size (also significantly negatively correlated with light establishment preference), and leaf shape (the leaf length/width ratio was significantly negatively correlated with light establishment preference). Based on this species classification, number of pioneers and non-pioneers could be determined in 71 plots of 0.3 ha, covering 11 common forest disturbance types in Southeast Asia. Three main patterns were detected with this methodology: (1) pioneer and non-pioneer densities were significantly correlated with the forest disturbance level; (2) pioneer densities decreased with time since disturbance; (3) pioneer densities increased with repeated disturbance. A sample size test indicated that forest disturbance in general, and the differences between the major disturbance types could be significantly determined with a minimum of five plots of 0.3 ha. An interactive version of the developed forest disturbance methodology is available at http://www.nationaalherbarium.nl/MacMalBorneo/index.htm.

Keywords: Southeast Asia; Borneo; Rapid assessment; Plant functional group; Plant morphology; Establishment preference; Forest disturbance; *Macaranga*; *Mallotus*

1. Introduction

Undisturbed lowland tropical forest is becoming increasingly rare and fragmented, especially in Southeast Asia, where its extent is already surpassed by secondary forest and agricultural land (Manokaran, 1992; Murali and Hedge, 1997; Sayer et al., 2000; Brooks et al., 2001). This has led to the situation that secondary forests now play a key role in the conservation of the lowland forests of Southeast Asia, especially in relation to the formation and persistence

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of forested corridors between the last remaining patches of undisturbed forest (Rijksen and Meijaard, 1999). However, the ecological quality of secondary forests can vary considerably, depending on the kind and severity of disturbance, the time elapsed since it took place, and the vicinity of undisturbed forest (Brown and Lugo, 1990; Corlett, 1994; Chazdon, 2003). For tropical forest management and conservation purposes, the development of reliable and simple methods that can quantify the severity of forest disturbance, and which can also be used to monitor forest recovery, would be useful.

One of the most obvious changes that takes place after disturbance in tropical forests is the sudden appearance of pioneer plant species (Brokaw, 1985; Nykvist, 1996; Guariguata and Ostertag, 2001; Slik et al., 2002, 2003; Slik and Eichhorn, 2003). The increase in pioneers in disturbed habitats is closely related to the increase in light levels in the forest understorey (Bazzaz and Pickett, 1980; Alvarez-Buylla and Martinez-Ramos, 1992; Pearson et al., 2002; Slik et al., 2002). Because pioneers increase in numbers after disturbance, they are, in principle, suitable for detecting and quantifying tropical forest disturbance (Slik et al., 2003). However, the discrimination between pioneer and climax species is not always that clear since they form the extremes of a continuous life history gradient (Swaine and Whitmore, 1988; Slik et al., 2003). Furthermore, the successional status of most species in the tropics is still unknown because of lack of ecological data. The use of morphological plant characteristics associated with the pioneer–non-pioneer life history strategy (Swaine and Whitmore, 1988; Alvarez-Buylla and Martinez-Ramos, 1992; Brzeziecki and Kienast, 1994) might be helpful to overcome this problem.

Here I focus on two common, species rich, and closely related plant genera of Southeast Asia belonging to the Euphorbiaceae (Webster, 1994): *Macaranga* Thou. and *Mallotus* Lour. The species in these two genera cover the complete life history gradient associated with forest disturbance (Primack and Lee, 1991; Davies et al., 1998), and have been shown to be good indicators for forest disturbance (Slik et al., 2003). My first objective is to determine if the morphology of these plants is correlating with their light establishment preferences. Three morphological characters that have been shown to be closely related to plant successional status were selected for this purpose: (1) wood density; (2) seed size; (3) leaf shape. Wood density was chosen because it is negatively correlated with tree growth rate (Thomas, 1996; Suzuki, 1999; Alder et al., 2002; ter Steege, 2003). It can thus be used to differentiate between slow and fast growers, which is one of the main criteria to discriminate between early and late successional species (Swaine and Whitmore, 1988). Seed size was included because it is negatively correlated with seed dispersal capability (Hammond and Brown, 1995; Westoby et al., 2002; Coomes and Grubb, 2003) and seed dormancy (Dalling and Hubbell, 2002), and positively correlated with shade-tolerance (Osunkoya et al., 1994; Hammond and Brown, 1995; Coomes and Grubb, 2003; Paz and Martinez-Ramos, 2003). These, again, are important criteria to discriminate between early and late successional species (Swaine and Whitmore, 1988). Leaf shape, defined here as the ratio between leaf length and width, was included because it is negatively related to leaf size and photosynthetic capacity of plants (Popma et al., 1992; Westoby et al., 2002; Falster and Westoby, 2003; Yanez-Espinosa et al., 2003), and, as such, forms a useful character to discriminate between early and late successional species.

My second objective is to classify the *Macaranga* and *Mallotus* species into pioneers and non-pioneers, using the three morphological characters discussed above. This classification will be used to determine the abundance of pioneers and non-pioneers in different types of disturbed forests. More specifically I want to know if pioneer and non-pioneer numbers are related to (1) general level of disturbance in a forest, (2) time since disturbance and (3) repeated disturbances. The outcome of these analyses will determine whether this methodology can indeed provide a useful tool for assessing forest disturbance in lowland tropical forests in Southeast Asia.

2. Material and methods

2.1. Field sites and measurements

Plots representing different disturbance types were established at several, climatologically similar, low-

Table 1
Disturbance types included in this study, time since disturbance, major area (see Fig. 1), and number of plots

Disturbance type	Time since disturbance (years)	Area	Plots (*n*)
Undisturbed		Berau	6
		ITCI	6
		Samboja	8
Burned once	1	ITCI	5
	3	ITCI	1
	3	Samboja	2
	15	Samboja	5
Burned twice	18, 3	Samboja	3
Burned repeatedly	15, 6, 3	Samboja	5
Logging followed by fire	15, 1	ITCI	5
Logged	1	ITCI	5
	3	Berau	1
	9	ITCI	1
	11	Berau	1
	16	ITCI	2
	17	ITCI	1
	18	ITCI	1
	19	ITCI	2
	25	ITCI	5
	29	ITCI	1
Logging followed by liberation thinning	21, 10	Berau	5

land (below 500 m altitude) dipterocarp forest locations in East Kalimantan, Indonesia (Table 1; Fig. 1). Each plot consisted of 30 subplots of 10 m × 10 m spread evenly along straight lines up to 900 m in length. Within each subplot hemispherical (fish-eye) canopy photographs were made at 2 m height in the centre of the subplot and all *Macaranga* and *Mallotus* species taller than 30 cm were identified up to species level, while the diameter of all individuals taller than 1.3 m was measured at breast height. Canopy photographs were analysed using WINPHOT (ter Steege, 1996) to calculate canopy openness values for each subplot.

2.2. Light establishment preferences of Macaranga and Mallotus species

Light establishment preference for *Macaranga* and *Mallotus* saplings (individuals between 0.3 and 3 m tall) was determined by assigning the canopy openness values measured in the subplots to the saplings encountered in those subplots. Species light establishment preferences were then calculated by taking the average canopy openness value of all the saplings per species.

2.3. Macaranga and Mallotus morphological characters

For each *Macaranga* and *Mallotus* species of which light establishment preferences were measured, I also determined leaf shape, seed size and wood density. Average leaf shape for each species was calculated by dividing leaf length by leaf width as measured from specimens present in the Nationaal Herbarium Nederland, Leiden University Branch, The Netherlands (NHN-L). Average seed size for each species was determined by measuring seed diameters from specimens present in the collections of the NHN-L. Average wood density (air dry) for each species was determined from literature (Burgess, 1966; Seng, 1990; Reyes et al., 1992; Soerianegara and Lemmens, 1993; Lemmens et al., 1995; Sosef et al., 1998; Suzuki, 1999) and measurements from wood samples stored in the collections of the NHN-L. Wood density of species for which neither literature data nor wood samples were available were estimated by averaging the wood densities of their nearest relatives based on existing classifications and phylogenies for *Macaranga* (Whitmore, 1975; Blattner et al., 2001; Davies, 2001) and *Mallotus* (Airy Shaw, 1975; Slik et al.,

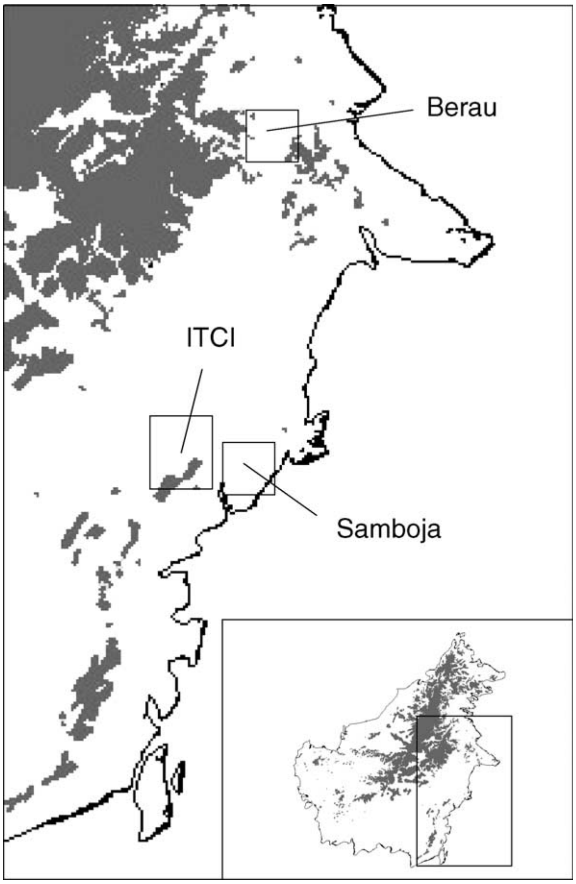

Fig. 1. Locations of the major research areas (see also Table 1).

2000). When the phylogenetic position of a species was unknown, it was given the average wood density value of the genus to which it belonged.

2.4. Relation between light establishment and morphology

The relation between light establishment values of the *Macaranga* and *Mallotus* species and their morphology was determined with simple regression analysis, using the computer program Statgraphics Plus for Windows 2.1, Statistical Graphics Corp., Rockville, MD, USA. Based on a number of possible relationships, this program indicates which curve fits the data best based on the highest R^2-value. All statistical analyses mentioned below were also performed with the use of Statgraphics Plus for Windows 2.1.

2.5. Classification of *Macaranga* and *Mallotus* species

Classification of *Macaranga* and *Mallotus* species into pioneers and non-pioneers was done by dividing each of the three morphological characters into three equal classes based on the range between the minimum and maximum value measured for each character. Classes were ordered from one to three in an order that reflected the change from pioneer to non-pioneer, i.e. from low to high leaf shape ratios, from small to large seed diameters, and from low to high wood densities. The average of the three class-values for each species was used to classify them into pioneers and non-pioneers, i.e. all species that had an average class-value ≤ 2 were classified as pioneer, while all species that had an average class-value >2 were classified as non-pioneer.

2.6. Suitability of the pioneer and non-pioneer classification for forest disturbance assessment

The classification of *Macaranga* and *Mallotus* species was used to determine the number of pioneers and non-pioneers in the plots surveyed in this study. Differences in pioneer and non-pioneer numbers between the studied forest disturbance types were determined with the use of a general linear model to compensate for differences in sample size, in combination with a post-hoc Fisher's least significant difference test. Data were log $10(n + 1)$ transformed to reduce data variance so that standard deviations became more comparable. Forest disturbance types were ordered according to the increasing percentage of pioneers to see how pioneer dominance was related to the disturbance history of the plots. The effects of time since disturbance and single versus repeated disturbances on pioneer and non-pioneer numbers in the plots was determined with Spearman rank correlations. These correlations were only performed for forests with comparable disturbance histories. Finally, a sample size determination test (described in Sokal and Rohlf (1995)) was used to determine the number of plots that have to be sampled to detect significant differences between the studied forest disturbance types. Data were log $10(n + 1)$ transformed for this test.

Table 2
Overview of the ecological and morphological characteristics of the species sampled in this study

Species	All individuals (n)	Canopy openness (%)	Wood density (g/cm^3)	Leaf shape (l/w)	Seed diameter (mm)	Class
Macaranga bancana	719	11.5	0.44	1.15	3.6	Pioneer
Macaranga beccariana	100	13.0	0.42	1.21	3.1	Pioneer
Macaranga conifera	382	13.0	0.42	1.67	3.2	Pioneer
Macaranga depressa	18	8.8	**0.48**	1.10	3.6	Pioneer
Macaranga gigantean	5956	24.8	0.37	0.99	2.8	Pioneer
Macaranga hosei	32	16.8	0.34	0.74	2.1	Pioneer
Macaranga hullettii	44	16.5	0.49	1.68	3.5	Pioneer
Macaranga hypoleuca	1073	17.6	0.34	0.79	3.1	Pioneer
Macaranga lamellate	18	4.0	0.58	1.68	6.8	Climax
Macaranga lowii var. *kostermansii*	508	5.7	**0.70**	3.36	4.5	Climax
Macaranga lowii var. *lowii*	2773	5.5	0.75	2.89	5.1	Climax
Macaranga motleyana	809	18.6	0.66	1.21	3.8	Pioneer
Macaranga pearsonii	4224	31.7	0.43	0.90	1.6	Pioneer
Macaranga pruinose	25	12.7	0.39	0.92	1.5	Pioneer
Macaranga rarispina	9	6.0	0.65	2.88	7.8	Climax
Macaranga recurvate	10	10.2	**0.42**	1.32	3.5	Pioneer
Macaranga repando-dentata	95	4.5	0.74	2.03	6.3	Climax
Macaranga tanarius	40	22.7	0.51	1.36	4.0	Pioneer
Macaranga trichocarpa	9978	19.4	0.54	1.35	3.7	Pioneer
Macaranga winkleri	397	30.0	0.34	1.46	0.9	Pioneer
Mallotus dispar	230	7.4	0.77	2.14	4.0	Climax
Mallotus eucaustus	130	3.0	**0.72**	3.20	4.1	Climax
Mallotus griffithianus	300	2.7	0.81	2.29	5.7	Climax
Mallotus lackeyi	297	13.7	0.79	1.58	5.1	Pioneer
Mallotus leucodermis	12	3.4	0.62	2.35	6.8	Climax
Mallotus macrostachyus	52	20.7	0.31	1.20	3.8	Pioneer
Mallotus miquelianus	976	12.2	0.82	2.93	4.3	Climax
Mallotus mollissimus	284	33.3	0.42	1.20	3.4	Pioneer
Mallotus muticous	41	3.7	**0.62**	2.01	6.5	Climax
Mallotus paniculatus	357	22.7	0.44	1.55	2.8	Pioneer
Mallotus peltatus	41	8.9	0.63	2.60	5.1	Climax
Mallotus penangensis	2400	6.1	0.62	2.80	5.0	Climax
Mallotus wrayi	519	6.3	0.76	2.83	5.8	Climax

Nomenclatural authorities for the species can be found in Slik et al. (2000) and at http://www.nationaalherbarium.nl/MacMalBorneo/index.htm. Light establishment preferences of the species were based on the average canopy openness under which their saplings were growing. Bold values in the wood density column indicate values that are estimated based on wood densities of their nearest relatives. Leaf shape is the ratio of leaf length and width. Classification of the species in pioneers and non-pioneers is based on their wood density, leaf shape and seed diameter (see Section 2.5).

3. Results

3.1. Relation between morphology and light establishment preferences

A total of 33 species of *Macaranga* and *Mallotus* were encountered in the 71 surveyed plots. Their light establishment preferences, seed sizes, wood densities and leaf shapes are shown in Table 2. The three morphological characters (wood density, seed size and leaf shape) were significantly related to the light establishment preferences of the studied species, i.e. there existed a clear pattern of decreasing seed size, wood density and leaf shape ratio with increasing light establishment preference of the species (Fig. 2). This relation was the strongest for seed size.

3.2. Classification of Macaranga and Mallotus species into pioneers and non-pioneers

Since the relation between light establishment preferences of the *Macaranga* and *Mallotus* species

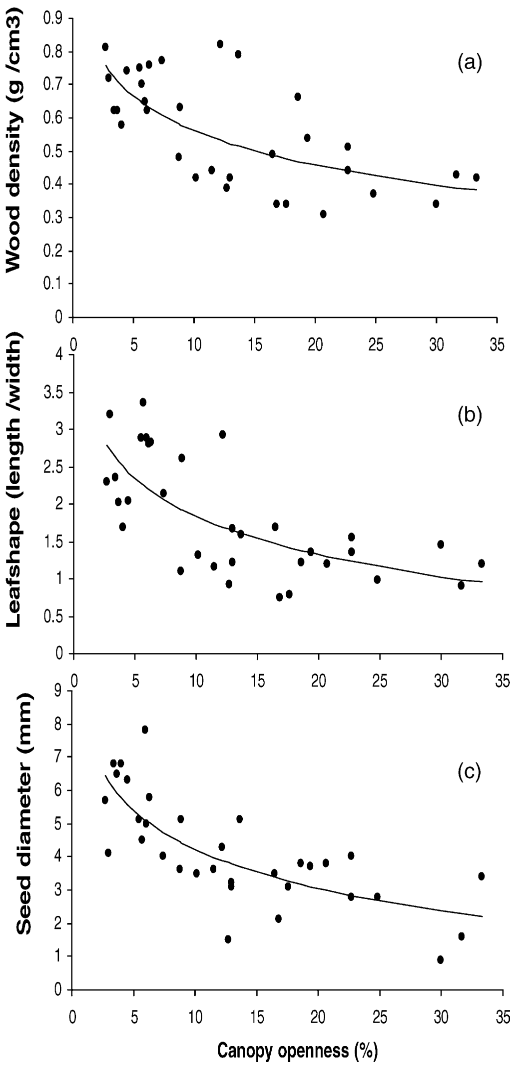

Fig. 2. Relation between light establishment preferences of the studied species and (a) wood density, (b) leaf shape, and (c) seed size. Wood density: $y = 0.91 - 0.15\ln(x)$; correlation coefficient (cc) = −0.68; $R^2 = 45.6$; F-ratio = 26.0; $P < 0.0001$. Leaf shape: $y = 3.52 - 0.73\ln(x)$; cc = −0.69; $R^2 = 47.7$; F-ratio = 28.3; $P < 0.0001$. Seed size: $y = 8.13 - 1.69\ln(x)$; cc = −0.76; $R^2 = 57.9$; F-ratio = 42.6; $P < 0.0001$.

and the three studied morphological characters was highly significant, these characters were used to divide them into pioneers and non-pioneers (Table 2). The ranges used for this classification are shown in Table 3. Twenty-one species were classified as pioneer (15 *Macaranga* and 4 *Mallotus*) and 14 as non-pioneer (5 *Macaranga* and 9 *Mallotus*).

Table 3
Class ranges used to classify species into pioneers and non-pioneers

Class	Wood density ($g\ cm^{-3}$)	Leaf shape (l/w)	Seed diameter (mm)
1	≤0.48	≤1.61	≤3.2
2	0.49–0.66	1.62–2.48	3.3–5.4
3	≥0.67	≥2.49	≥5.5

The class order reflects the change from a pioneer to a climax life history strategy.

3.3. Suitability of the pioneer and non-pioneer classification for forest disturbance assessment

A clear pattern of increasing pioneer dominance with increasing level of disturbance was visible for the studied plots (Table 4). Time since disturbance had a significant negative effect on pioneer dominance for logged and burned forests (Spearman-rank correlation of −0.66, d.f. = 20, $P = 0.004$ for pioneer numbers versus time since logging category; and −0.70, d.f. = 13, $P = 0.015$ for pioneer numbers in once burned forest versus time since disturbance category). Additionally, repeated disturbances had a significant positive effect on pioneer tree numbers (Spearman-rank correlation of 0.58, d.f. = 21, $P = 0.009$ for forests that burned once and repeatedly and were measured 3 years after the last fire took place).

The range in pioneer and non-pioneer tree numbers for the separate plots per disturbance type was high (see min.–max. ranges in Table 4), indicating that single 0.3 ha plots are too small to determine the disturbance level in a forest with certainty. In Table 5, the required number of plots needed to detect significant differences between all combinations of forest disturbance types studied are shown (based on pioneer tree numbers only). It shows that relatively few plots (3–6) are needed to differentiate between the main forest disturbance types.

4. Discussion

4.1. The relation between morphology and successional status of Macaranga and Mallotus species

Many studies in tropical forests have shown that plant morphology is closely related to shade and sun

Table 4
The relation between pioneer and non-pioneer abundance (*n* per plot of 0.3 ha) and disturbance type (time since disturbance between brackets)

Disturbance type	Pioneers ($n \pm$ S.D.)	Non-pioneers ($n \pm$ S.D.)	Pioneers (%)	Pioneer range (min.–max.)	Non-pioneer range (min.–max.)
Undisturbed	23.5 ± 36.4a	250.8 ± 143.4a	8.6	1–151	6–465
Logged (21) and thinning (12)	11.6 ± 9.6a	51.8 ± 37.5bc	18.3	4–27	26–113
Logged (20–30)	35.3 ± 21.6b	82.3 ± 69.9bc	30.0	19–78	2–180
Logged (10–20)	58.4 ± 44.4bc	80.3 ± 110.9bc	42.1	20–142	10–324
Logged (0–10)	138.4 ± 130.0cd	110.0 ± 78.8ab	55.7	42–376	5–196
Once burned (15)	168.2 ± 82.1de	45.6 ± 20.0bcd	78.7	82–269	15–68
Once burned (3)	507.0 ± 273.8ef	57.0 ± 39.7abcd	89.9	241–788	15–94
Once burned (1)	476.0 ± 229.3ef	16.2 ± 12.6cde	96.7	249–798	1–34
Thrice burned (3)	1124.6 ± 662.0f	35.0 ± 29.2bcd	97.0	611–2269	6–74
Twice burned (3)	1671.7 ± 1275.3f	8.3 ± 4.9de	99.5	612–3087	5–14
Logged (15) and burned (1)	1264.2 ± 866.3f	6.0 ± 7.3e	99.5	173–2191	0–17
d.f.	70	70			
F-ratio	24.9	7.0			
P	<0.0001	<0.0001			

Disturbance types are ordered according to increasing dominance of pioneers. Significant differences in pioneer and non-pioneer numbers (log transformed) between disturbance types (indicated with different characters) were tested using a general linear model with a Fishers' least significant difference test.

tolerance (Bongers and Popma, 1990; Osunkoya and Ash, 1991; Osunkoya et al., 1992, 1994; Popma et al., 1992; Pearson et al., 2002; ter Steege, 2003). This study adds new evidence to these earlier results by finding very strong and significant associations between wood density, leaf shape, and seed size, and the light conditions under which saplings of *Macaranga* and *Mallotus* species were found growing. Since light establishment preference, i.e. sun and shade tolerance of species, is one of the most accepted measures of plant successional status (Swaine and Whitmore, 1988), the strong relation between light establishment preference and the three studied morphological characters means that these characters can be used to determine the successional status of *Macaranga* and *Mallotus* species in the absence of ecological field data. Since ecological data are still lacking for most species, this information is very useful, and, in principle, makes it possible to expand this study to all *Macaranga* and *Mallotus* species occurring in Southeast Asia.

The results of this study also confirm, although indirectly, some of the classical distinctions that have been used to differentiate between early and late

Table 5
Sample sizes (number of 0.3 ha plots) needed to detect significant differences between all possible combinations of forest disturbance types included in this study (based on pioneer numbers only)

	1	2	3	4	5	6	7	8	9	10
1. Undisturbed										
2..Log-thin	460									
3. Logged (20–30)	5	4								
4. Logged (10–20)	5	4	32							
5. Logged (0–10)	4	4	9	18						
6. Once burned (15)	3	3	4	5	17					
7. Once burned (3)	3	3	3	3	4	6				
8. Once burned (1)	3	3	3	3	4	5	1094			
9. Thrice burned (3)	2	2	3	3	3	3	7	6		
10. Twice burned (3)	3	3	3	3	4	4	8	8	82	
Logged (15) and burned (1)	3	3	4	4	5	6	27	24	1217	79

Numbers in the row headings correspond to numbers in column headings. For exact descriptions of the disturbance types see Table 1.

successional species (Swaine and Whitmore, 1988). Wood density, which is negatively related to growth rate (Thomas, 1996; Suzuki, 1999; Alder et al., 2002; ter Steege, 2003), decreased with light establishment preference, indicating that most fast growers established under high light conditions. Furthermore, seed size decreased with increasing light establishment preference. Since seed size is negatively related to seed dispersal capability (Hammond and Brown, 1995; Westoby et al., 2002; Coomes and Grubb, 2003) and seed dormancy (Dalling and Hubbell, 2002), this indicates that species with good seed dispersal and dormancy capabilities, generally need high light conditions for successful establishment. Seed size was also found to be positively related to light conditions during establishment, thus confirming earlier observations (Osunkoya et al., 1994; Hammond and Brown, 1995; Coomes and Grubb, 2003; Paz and Martinez-Ramos, 2003). Additionally, leaf shape, i.e. the ratio between leaf length and width, decreased with increasing light establishment preference, indicating that leaves of species that prefer high light conditions were relatively wider than those of shade preferring species. This change in leaf shape is closely related to leaf size and photosynthetic capacity of plants, which have been shown to increase with light availability (Popma et al., 1992; Westoby et al., 2002; Falster and Westoby, 2003; Yanez-Espinosa et al., 2003).

Most pioneers belonged to the genus *Macaranga*, while most non-pioneers belonged to the genus *Mallotus*. This is in agreement with earlier observations by Primack and Lee (1991) and Slik et al. (2003). It possibly indicates some degree of niche differentiation between these two closely related genera. Interestingly in this respect is the fact that the *Mallotus* species that have been classified as pioneers are also the ones that are most closely related to the genus *Macaranga* (Blattner et al., 2001; Slik and van Welzen, 2001).

4.2. Successional status classification as a tool for measuring forest disturbance

Three main trends were identified in this study: (1) pioneer and non-pioneer density are closely related to forest disturbance level; (2) pioneer density decreases with time since disturbance; (3) pioneer density increases after repeated disturbance. Most of these trends were only significant for pioneers and not for non-pioneers. This is probably related to the fact that non-pioneer density in plots is not only dependent on disturbance level, but also on pre-disturbance density. Since the effect of disturbance cannot be disentangled from the effect of pre-disturbance density, the use of only non-pioneers as indicators of forest disturbance is not advisable (unless post- and pre-disturbance data are available). Since pioneer establishment is almost exclusively dependent on disturbance, simply because pioneers usually do not recruit in the closed forest understorey, pioneer density is a much more reliable measure of forest disturbance.

Although application of the pioneer and non-pioneer classification yields results which can be used to determine forest disturbance, the results also show that the variation in pioneer and non-pioneer numbers in similar disturbance types can be very large. Sample size testing indicates that for reliable detection of disturbance and differentiation between the major disturbance types included in this study (undisturbed, logging, fire, repeated disturbance), a sample size of at least five plots is required. These plots should preferably be spread randomly over the forest type under study to capture as much of the variation in pioneer and non-pioneer numbers as possible. Unfortunately, significant differentiation between disturbance levels within the major forest disturbance types, such as between logged forests of different ages, different types of burned forest, and between different kinds of repeatedly disturbed forests, sometimes requires unfeasibly large sample sizes.

Although most repeatedly disturbed forests showed the highest number of pioneers in combination with the lowest number of non-pioneers of all forest disturbance types, there was one exception to this rule. Logged forests, which had subsequently been subjected to understorey liberation thinning showed very low pioneer densities. Liberation thinning in Indonesia is focussed on removal of seedlings and saplings of non-commercial tree species, including pioneer tree species (Fadillah, 2000; Kammesheidt et al., 2003). This means that liberation thinning, which is generally applied in logging concessions in Indonesia since the early 1990s, destroys the disturbance information that is potentially present in the species composition of logged forests. As a consequence, no reliable disturbance estimate can be determined for this type of forest disturbance with the methodology developed here.

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