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Effects of seed availability, site conditions, and herbivory on pioneer recruitment after logging in Sabah, Malaysia

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Abstract

Woody pioneers invade disturbed tropical forests but can be patchily distributed. We investigated causes of this patchiness in selectively logged forests near the Danum Valley Field Centre (DVFC) in Sabah, Malaysia.

In a recently logged forest, we compared seed sources and seedling establishment between two logging systems (conventional practices [CL] and reduced impact logging [RIL]) and between two soil disturbance classes (topsoil or subsoil exposed). Tree seeds were less abundant than shrub and treelet seeds, and seed banks contributed many more viable seeds than did seed rain. Topsoil removal reduced seed and seedling counts and growth rates of planted seedlings. More pioneer seedlings established on RIL than on CL plots, but survival of planted seedlings was lower under RIL, perhaps due to denser canopy cover. Broadcasting seeds increased seedling recruitment for five animal-dispersed pioneer trees but not for two wind-dispersed trees.

Longer term survival and growth of pioneer seedlings were compared between logging gaps (canopy but not soil disturbed) and skid tracks (canopy and soil disturbed) at a second site. Relative numbers in gaps vs. skid tracks varied by species, but across species, seedlings grew 40% more rapidly in gaps than in skid tracks. Survivorship differed among species but not between habitats. The three most common species experienced >95% mortality within 42 months.

At a third site, we compared effects of mammalian herbivores on pioneer seedling performances in exclosures and open (control) plots centered at the edge of recently abandoned skid tracks. Fewer pioneer seedlings established in skid tracks than in less-disturbed edges, but abundances did not differ between exclosure and control plots. Over 18 months, pioneers survived better and grew on average 44% taller with mammalian herbivores excluded.

Pioneer colonization can be seed limited, but high seedling mortality, exacerbated by herbivore damage, can limit recruitment even when seeds are available.

Keywords: Danum Valley Field Centre; *Macaranga*; *Neolamarckia*; Pioneer trees; Seed bank; Seed rain; Seedling recruitment; Selective logging; Soil disturbance; Tropical rain forest; Vertebrate herbivory

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1. Introduction

Woody pioneer plants are common elements of logged dipterocarp forests of southeast Asia (Whitmore, 1984; Primack and Lee, 1991), but their distributions exhibit considerable spatial patchiness (Abdulhadi et al., 1981; Cannon et al., 1994; Howlett, 1998). Components of early succession after natural disturbances, these species also may provide ecosystem services that promote the recovery of selectively logged forests (Brown and Lugo, 1990). If so, it is important to understand the factors contributing to their

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spatial patchiness. To identify limits to recruitment of woody pioneer species in logged tropical forests of Sabah, Malaysia, we investigated effects of seed availability, site conditions, logging systems and vertebrate herbivory on establishment, growth and mortality of these species.

Woody pioneers, including trees, shrubs and lianas, are fast-growing species whose abundant and widely dispersed seeds require high-light conditions for germination and establishment (Whitmore, 1983; Swaine and Whitmore, 1988). Natural forests contain only scattered individuals of woody pioneers in or near current or previous canopy gaps (Whitmore, 1984; Primack and Lee, 1991). Pioneers are most abundant in the largest treefall gaps (Brokaw, 1987; Hubbell et al., 1999) and, within gaps, are concentrated in areas with soil disturbance (Putz, 1983; Nuñez-Farfan and Dirzo, 1988). By creating canopy openings and disrupting soils, anthropogenic disturbance provides opportunities for recruitment by pioneers, and these species occur at high densities in secondary forests (Brown and Lugo, 1990). Some forms of soil disturbance favor pioneer establishment (Abdulhadi et al., 1981; Uhl et al., 1982; Davies et al., 1998), but more intensive soil disturbance, such as that associated with bulldozer traffic, can limit local recruitment (Uhl et al., 1982; Nussbaum, 1995; Guariaguata and Dupuy, 1997). Because pioneer species differ in their responses to canopy and soil disturbance, they may differ also in their abundance patterns after natural and anthropogenic disturbances (Brokaw, 1987; Nuñez-Farfan and Dirzo, 1988; Davies et al., 1998; Howlett, 1998).

Seed availability, establishment success, and seedling survival all can limit recruitment into open sites within plant communities (Schupp et al., 1989; Schupp, 1995; Dalling et al., 1998), and optimum sites for seeds may not be suitable for seedlings (Schupp, 1995). Seed availabilities might be constrained by small local populations of mature pioneers, by seasonal hiatuses in seed production, or by reductions in the seed bank due to topsoil removal or seed burial by the operation of logging machinery. In addition, logging activities could create patches with unfavorable site conditions that produce slow seedling growth and high mortality. Moreover, if pioneer taxa differ in their abilities to establish under particular site conditions, then only a subset of disturbed sites may be suitable for individual pioneer species. Finally, vertebrate herbivores, a number of which reach unnaturally high densities in logged forests (reviewed by Grieser Johns, 1997), could affect early successional dynamics by preferentially grazing or browsing relatively poorly defended pioneer tree seedlings (Coley et al., 1985; Davidson, 1993).

To investigate potential roles of seed sources, site factors and herbivory in limiting recruitment of woody pioneers into recently logged habitats, we measured existing soil seed banks, post-logging seed rain, seedling establishment and growth, and vegetative cover after 1 year. We added seeds of pioneer trees to assess seed limitation and planted pioneer tree seedlings to determine seedling performances. We compared these measures between disturbed sites with topsoil exposure and those with subsoil exposure, and between sites logged by conventional methods (CL) and those logged by reduced impact logging (RIL) techniques. In a population of woody pioneer saplings established in a different recently logged forest, we observed survival and growth during 3.5 years. Finally, in a third logged forest, we investigated the effects of vertebrate herbivores on woody pioneer colonization, growth, and survival.

2. Site descriptions

We based our study at the Danum Valley Field Centre (DVFC) in Sabah, Malaysia. DVFC (4°58′N, 117°48′E) adjoins the 438 km^2 Danum Valley Conservation Area in the midst of a 10^6 ha forest concession reserved for timber production (Marsh and Greer, 1992). Vegetation is primarily lowland dipterocarp forest (Newbery et al., 1992) on rolling to steep terrain ranging from 200 to 1000 m elevation. Soils and geology are extremely variable, both locally and regionally (Marsh and Greer, 1992; Nussbaum, 1995). DVFC receives approximately 2700 mm of rainfall each year (Walsh and Newbery, 1999). Although all months average >100 mm of rainfall, relatively dry periods occur in March–April and in August–September (Marsh and Greer, 1992; Walsh and Newbery, 1999). Mean daily minimum temperatures are around 22 °C with little seasonal fluctuation, while mean daily maxima range from 29 °C during December–February to 32 °C during the drier months of April and September (Walsh and Newbery, 1999).

In Sabah, natural forests are logged selectively, with harvest of up to 15 stems per hectare of commercial species larger than 60 cm diameter (Sabah Forestry Department, 1989; Pinard and Putz, 1996). Logs are typically extracted with bulldozers, which can compact or churn 17–40% of the soil surface (Abdulhadi et al., 1981; Jusoff and Majid, 1992; Nussbaum et al., 1995; Pinard et al., 2000). Logged forests are a heterogeneous mosaic of remnant and disturbed forest patches, interlaced with roads and bulldozed tracks (Cannon et al., 1994; Nussbaum, 1995; Howlett, 1998; Pinard et al., 2000).

We chose areas logged in 1991, 1992, and 1993 for different parts of this study. Our site names refer to the year of logging (e.g., Coupe93 was logged in 1993). Each annual coupe is further divided into numbered blocks of approximately 50 ha, demarcated by logging crews. Coupe91 includes two disjunct sections, both northeast of DVFC (Pinard et al., 1996). Coupe92 and Coupe93 lie west of DVFC, on opposite sides of a ridge. Coupe93, bordering the Segama River 10 km upstream from DVFC, includes the RIL trial area. Compared with conventional practices (CL), RIL involves additional planning and greater control of felling and skidding operations, and it disturbs less soil and canopy area (Pinard and Putz, 1996; Pinard et al., 2000).

3. Methods

3.1. Pioneer seed sources and establishment limitations

3.1.1. Experimental layout

In the Coupe93 RIL area, we focused on two soil disturbance classes within each of three CL blocks and three RIL blocks. Jusoff and Majid (1992) presented a five-category classification (based on Murphy, 1982) of soil disturbance resulting from logging; we selected the two classes that are colonized naturally by substantial numbers of pioneers (Howlett, 1998). In both CL and RIL blocks, we placed half of our plots in areas where topsoil had been exposed (DC2). Light scraping with the skidder blade, or pushing a tree across a site, removed pre-existing litter and vegetation or mixed it into topsoil. Remaining plots were located in areas, such as multiple-pass skid tracks, where subsoil had been exposed by removal of litter and topsoil (DC3).

We laid out a total of ninety-six 2 m × 2 m plots, evenly divided among the two soil disturbance classes and two logging treatments. Pair of plots were dispersed along skid tracks by using a random number table to select between-pair distances ranging from 20 to 100 m. At each selected location, one plot was placed in the nearest area of DC2 disturbance, and a second in the nearest area of DC3 disturbance, at least 1 m but not more than 7.5 m distant. For each plot, we estimated canopy cover with a spherical densiometer (Forestry Suppliers, Jackson MS, USA) and measured soil strength, an indicator of soil compaction, as the mean of five haphazardly distributed soil penetrometer readings.

Each plot was divided into four 1 m × 1 m subplots. Natural seedling establishment was recorded in two diagonally opposite "control" subplots. To test whether pioneer establishment was limited by seed availability, pioneer tree seeds were added to the "seed-addition" subplot, which was surface-scarified to hold seeds. In the final, "seed-availability" subplot, soil seed banks and seed rain were assessed and pioneer tree seedlings were planted.

3.1.2. Soil seed bank

In every seed-availability subplot, we collected and combined five 10 cm × 10 cm × 2.5 cm deep soil cores. Pooled subsamples were spread in a 1 cm thick layer on sand-filled germination beds in the DVFC nursery. Transparent plastic covers over the germination beds prevented contamination from seed rain, and control samples tested for seeds in the substrate. Seedlings germinating within 6 months were identified to species, counted, and removed.

3.1.3. Seed rain

Four seed traps, polyethylene seedling bags folded into flexible trays 20 cm × 20 cm × 10 cm deep, were partially buried in each seed-availability subplot. A mixture of screened river sand and composted sawdust (to retain moisture) filled each trap to a depth of 2.5 cm. Seed traps were placed in the field in early October 1993, just prior to the annual peak in seed dispersal by *Macaranga* spp. (B.E. Howlett, unpublished data).

Six weeks later, the soil from all four traps in each plot was collected, pooled, and placed in covered germination beds. Soil samples were spread 1 cm thick on top of a 2.5 cm layer of screened river sand. Seedlings emerging within 6 months were identified to species, counted, and removed.

3.1.4. Seed addition

We added pioneer tree seeds to seed-addition subplots and compared seedling establishment with natural establishment in control subplots. For *Macaranga indistincta*, *M. pearsonii*, *M. gigantea*, *M. hypoleuca*, and *Trema tomentosa*, which produce relatively large, animal-dispersed seeds, 20 seeds of each species were added to every plot. Since *Macaranga* seeds can have low viability, ranging among species from 2 to 30% (B.E. Howlett, unpublished data), we concentrated viable seeds from a bulk collection by discarding seeds that floated in water. Previous germination tests found more than 50% viability for seeds that sank, while seeds that floated were generally hollow seed coats. Approximately 100 *Duabanga moluccana* seeds and 200 *Octomeles sumatrana* seeds also were added to every plot; these wind-dispersed seeds are too small to count reliably, so estimates were based on volume. Every 4 months for 1 year, we identified, mapped, and tagged woody plant seedlings appearing in control and seed-addition subplots.

3.1.5. Seedling performance

We transplanted screenhouse-grown seedlings of pioneer tree species to the field and assessed their survival and growth. Five seedlings, one each of *D. moluccana*, *M. pearsonii*, *M. gigantea*, *Neonauclea longipedunculata*, and *O. sumatrana*, were planted into each of the 96 plots. Due to the time necessary to raise seedlings, transplanting was delayed until March 1994. Seedling survivorships and heights were recorded eight months later, 1 year after logging.

3.1.6. Vegetative cover

At the end of 1 year, we measured vegetative cover in each study plot. For every 20 cm × 20 cm grid square within control and seed-addition subplots (25 points each), we recorded the dominant lifeform, including: (1) graminoids and herbs, (2) herbaceous and woody vines, (3) woody pioneers, and (4) other (non-pioneer or unknown woody species).

3.1.7. Statistical analyses

All analyses were performed using JMP 3.2 (SAS, 1995). Analysis of variance (ANOVA) compared canopy densities and log-transformed soil strengths between soil disturbance classes (topsoil or subsoil exposure), between logging systems (RIL or CL) and among blocks nested within logging system. Ordinal-logistic regression compared seed or seedling abundances between seed sources (bank or rain), soil disturbance classes and logging systems. Frequent zeroes in the seed and seedling counts prevented full utilization of the paired design, and species were grouped into two lifeforms: shrubs and treelets (maximum mature height <10 m), and medium to large trees (maximum height >10 m).

For each seeded species, we calculated differences in seedling density between seed addition and control subplots. Ordinal-logistic regressions compared these differences between soil disturbance classes and logging systems, as well as among blocks within logging system. To evaluate patterns for individual species, seedling densities of each species were pooled across levels of all non-significant factors and compared between control and seed-addition subplots with Wilcoxon signed-ranks tests. To correct for multiple (seven) species comparisons, P-values were adjusted by the sequential-Bonferroni technique to a tablewide $\alpha = 0.05$ (Rice, 1989). Similarly, differences in seedling densities after the first year were compared between seed addition and control subplots, considering only seedlings that survived to the end of the year.

For planted seedlings, ANOVA compared log-transformed 1-year heights of surviving seedlings among species, logging systems, soil disturbance classes, and blocks nested within logging system. Seedling survivorships were compared among species, disturbance classes, logging systems, and blocks nested within logging system by a log-linear model.

Repeated-measures MANOVA compared vegetative cover by woody pioneers in seed addition and control subplots and determined whether data could be pooled. Combining data from the two types of subplots to give a single value for each life form in every plot, we then compared cover values among the four lifeforms. In both of these analyses, independent variables included soil classes, logging systems, and blocks within logging system.

3.2. Pioneer demography

In four blocks of Coupe91, we recorded pioneer seedling survival during 42 months. In an earlier study assessing seed vs. site limitations on pioneer recruitment (Pinard et al., 1996), we tagged naturally established pioneer seedlings in seventy-two 2 m × 5 m plots dispersed across four blocks. In each block, nine 10 m^2 plots were established on each of two habitat types defined by logging disturbance. The two habitat types were related, but not identical, to soil disturbance classes used in the seed availability study. In "gap" plots, the canopy had been removed and woody debris may have been added, but little soil disturbance occurred. This disturbance category equates to class DC1 of Jusoff and Majid (1992), where a disturbed litter layer is still present. "Skid" plots received soil disturbance and compaction from bulldozer traffic. These sites typically were DC3 (subsoil exposed), but they could have been DC2 (topsoil exposed) or DC4 (subsoil exposed and compacted), depending on the amount of traffic and subsequent erosion. We recorded abundances and survivorships of pioneer tree species colonizing these plots. At 6-month intervals for 42 months after logging, we tagged, censused and measured all pioneer tree seedlings more than 50 cm tall.

Seedling abundances were compared between habitat types and among blocks with logistic regression. Species abundances were dependent variables, and habitat types and blocks were independent variables. To examine patterns by species, *G*-tests compared individual species' abundances between gaps and skids. To adjust for the 12 separate comparisons, *P*-values were corrected to a tablewide $\alpha = 0.05$ (Rice, 1989). Log-transformed 1-year seedling heights were compared among species, blocks, and habitat types by ANOVA. Interaction terms that included species were not calculated because several species did not occur in all blocks and habitat types. Survival times were compared among blocks, habitat types, and species with a proportional hazards (Cox) survival model (Cox and Oakes, 1984).

3.3. Effect of mammalian herbivores on pioneer communities

To investigate effects of mammalian herbivores, particularly sambar deer (*Cervus unicolor*), on pioneer colonization of logged forests, we constructed six pairs of chicken-wire exclosures on recently abandoned skid roads. We established this experiment in Coupe92 about 1 year after logging. Each 4 m × 6 m × 1.5 m tall exclosure was oriented parallel to a skid track and centered on the track edge. Half of each plot lay on the skid track where subsoil was exposed (in DC3 habitat), and half on the less-disturbed edge where topsoil was exposed (DC2 habitat). Each plot pair included an exclosure plot and an open control. A fence completely surrounded each exclosure, while 2 m wide openings at both ends of open controls allowed terrestrial browsers to enter. At 2–6-month intervals for 18 months after exclosure construction, we identified, tagged, and mapped pioneer seedlings, and recorded their heights. During every census, we inspected and maintained the exclosures and cut vines or branches encroaching on the fences.

The five most common pioneer taxa were considered separately, while remaining seedlings were categorized as other trees or shrubs. Logistic regression compared counts by pioneer species among replicate plot pairs, exclosure treatments (open vs. exclosure), and soil disturbance classes (DC2 vs. DC3). Log-transformed 1-year seedling heights were compared among taxa, exclosure treatments, and soil disturbance classes by split-plot ANOVA. Plot was nested within exclosure treatment and soil disturbance class and considered a random effect. Survival was compared among plots, taxa, 1-year seedling heights, exclosure treatments, and soil disturbance classes with a proportional hazard survival model.

4. Results

4.1. Pioneer colonization

4.1.1. Canopy cover and soil strength

Initial canopy cover differed significantly among blocks within logging system ($F = 4.0$, d.f. $= 4$, $P = 0.005$) and between logging systems ($F = 21.7$, d.f. $= 1$, $P < 0.0001$), but not between soil disturbance classes ($P = 0.24$). RIL plots exhibited an average of 60% canopy cover, compared with 42% in CL plots. In contrast, soil strength did not differ significantly between logging systems ($P = 0.15$) or among blocks within logging system ($P = 0.91$), but was 2.5 times

Table 1
Densities (seedlings × m^{-2}) of pioneer seedlings, by taxon or lifeform, establishing in seed bank samples (total of 1.2 m^2), seed rain samples (total of 6 m^2), and in test plots in Coupe93 (total of 72 m^2)

Taxon	Lifeform	Seed bank				Seed rain				Established seedlings			
		DC2		DC3		DC2		DC3		DC2		DC3	
		CL	RIL	CL	RIL	CL	RIL	CL	RIL	CL	RIL	CL	RIL
All shrubs and treelets		150	168	33	47	11.0	5.3	8.8	2.7	7.2	11.7	1.2	3.0
All trees[a]		98	208	21	64	1.8	2.2	1.2	1.2	1.4	3.5	1.1	3.0
Uncaria spp.	Liana	171	99	34	49	0	0	0.5	0.2	–	–	–	–
C. longifolia	Shrub	21	49	5	13	0.2	0.2	0.5	0.2	2.2	3.9	0.4	0.7
Melastomataceae	Shrub	10	14	5	6	2.2	0.8	1.5	0.5	0.3	0.1	0	0.1
Ficus spp.	Treelet	15	12	4	8	1.5	0.3	1.3	0	0.3	0.9	0	0.2
M. winkleri	Treelet	3	3	1	2	0	0	0	0	2.1	4.4	0.8	1.5
Urticaceae	Treelet	82	76	13	13	7.5	3.8	4.8	1.8	1.4	1.3	0.2	0.2
N. cadamba	Tree	34	12	8	15	0.7	0.2	0	0.2	0.5	1.1	0.7	1.6
Neonauclea spp.	Tree	4	13	3	11	0.3	0.7	0.7	0.2	0.1	0.3	0.1	0.4
O. sumatrana	Tree	39	163	3	26	0.2	0.7	0	0	0.1	0.3	0	0.1

[a] Includes seeded species established in control subplots.

greater in DC3 plots than in DC2 plots ($F = 2.0$, d.f. $= 1, P < 0.0001$). Interaction effects were not significant for either canopy cover or soil strength.

4.1.2. Seed bank and seed rain

Seed bank contributed substantially more viable seeds than did seed rain (Table 1). The most abundant taxon was *Uncaria* (Rubiaceae), a locally common group of lianas. *O. sumatrana* was the most abundant pioneer tree species, but a single sample contained more than one-third of its seeds. Seed rain also was markedly patchy, with most taxa collected in just a few plots. The most abundant taxon, Urticaceae, containing several species of large shrub (e.g., *Astrothalamus reticulata*, *Boehmeria* sp., *Leukosyke capitella*, and *Pipturus argenteus*), contributed on average just one seed to each seed rain sample. However, one-fifth of all *Pipturus* seeds landed in a single plot.

Tree seeds were much less numerous, and their occurrences less frequent, than were seeds of treelets and shrubs (Table 1). Seeds were much more abundant in seed banks than in seed rain (shrubs and treelets: LR $\chi^2 = 76.9$, d.f. $= 1, P = 0.0000$; trees: LR $\chi^2 = 85.8$, d.f. $= 1, P = 0.0000$), were more abundant in DC2 than in DC3 plots (shrubs and treelets: LR $\chi^2 = 17.4$, d.f. $= 1, P = 0.0000$; trees: LR $\chi^2 = 16.9$, $d.f. = 1, P = 0.0000$), and were more abundant in RIL than in CL plots (shrubs and treelets: LR $\chi^2 = 5.2$, d.f. $= 1, P = 0.023$; trees: LR $\chi^2 = 5.3$, d.f. $= 1$, $P = 0.022$). For shrubs and treelets, seed abundances differed among blocks (LR $\chi^2 = 11.4$, d.f. $= 4$, $P = 0.023$), and seed source showed a significant interaction with logging system (LR $\chi^2 = 39.9$, d.f. $= 1, P = 0.0000$). Although seed banks were similar in CL and RIL plots, lower seed rain under RIL led to a greater excess of seed bank over seed rain in RIL than in CL blocks. Other interaction terms were not significant. In the tree model, no interaction term was significant.

4.1.3. Pioneer establishment

Few seedlings of large pioneer trees colonized control subplots (Table 1). In contrast, *Macaranga winkleri*, a streamside pioneer treelet, and *Callicarpa longifolia*, a scandent shrub, were abundant. These two species accounted for almost half of all pioneer seedling establishment. Both for trees and for shrubs and treelets, total numbers of established seedlings were greater in DC2 plots than in DC3 plots (trees: LR $\chi^2 = 4.0$, d.f. $= 1, P = 0.045$; shrubs and treelets: LR $\chi^2 = 59.0, P < 0.0001$), greater in RIL blocks than in CL blocks (trees: LR $\chi^2 = 15.1$, d.f. $= 1, P = 0.0001$; shrubs and treelets: LR $\chi^2 = 13.7, P < 0.0001$), and heterogeneous among blocks within logging system (trees: LR $\chi^2 = 22.4$, d.f. $= 4, P = 0.0002$; shrubs and treelets: LR $\chi^2 = 18.0, P = 0.0012$).

Table 2
For species whose seeds were added to the study plots, number of established seedlings in Coupe93 by treatment, logging system, and soil disturbance class. Summed over 24 plots (total of 48 m^2 for controls, 24 m^2 for seed-addition subplots)

Species	DC2 (topsoil exposed)				DC3 (subsoil exposed)			
	CL		RIL		CL		RIL	
	Control	Seeded	Control	Seeded	Control	Seeded	Control	Seeded
Duabanga moluccana	11	13	11	18	2	11	6	17
Macaranga gigantea	2	31	2	18	1	16	1	16
M. hypoleuca	3	10	3	18	2	8	0	9
M. indistincta	2	12	8	24	2	8	9	15
M. pearsonii	2	11	4	9	3	10	0	6
Octomeles sumatrana	8	4	25	16	0	1	6	8
Trema orientalis	0	6	4	0	2	8	2	1

4.1.4. Seed addition

Results of seed addition did not differ significantly by either logging system or soil disturbance class ($P > 0.40$ in all cases), so data were pooled across categories. For five of seven pioneer tree species, seed addition significantly increased total seedling numbers (Table 2; *Duabanga*: $\chi^2 = 312$; *M. gigantea*: $\chi^2 = 558$; *M. hypoleuca*: $\chi^2 = 244$; *M. indistincta*: $\chi^2 = 476$; *M. pearsonii*: $\chi^2 = 262$; all corrected $P < 0.0001$). After 1 year, these species continued to show significantly higher densities in seed-addition subplots compared to control subplots (all corrected $P < 0.0001$).

4.1.5. Vegetative cover

Percent cover by woody pioneers did not differ between control and seed-addition subplots (MANOVA contrast; whole model: $F = 0.73$, d.f. $= 14$, 170, $P = 0.74$), and values for these three subplots were combined to give a single cover value in each plot. Vegetative cover (Model: Wilk's $\lambda = 0.76$, $F = 3.9$, d.f. $= 7, 86$, $P = 0.0009$) differed among lifeforms (Table 3; $F = 18, \text{d.f.} = 3, 84, P < 0.0001$) and among blocks within logging system ($F = 4, \text{d.f.} = 1, 86, P = 0.0052$), and was greater in DC2 plots than in DC3 plots ($F = 8, \text{d.f.} = 1, 86, P = 0.0054$). Additionally, a trend for greater cover in RIL areas, compared with CL areas, was marginally significant ($F = 3$, $\text{d.f.} = 1, 86, P = 0.074$). Lifeforms exhibited different patterns across soil disturbance classes, as indicated by a significant lifeform by soil disturbance class interaction ($F = 14, \text{d.f.} = 3, 84, P < 0.0001$). Vegetative cover in DC2 areas exceeded that in DC3 areas, but both herbs (including grasses and sedges) and vines displayed the reverse pattern (Table 3). Other two- and three-way interactions were not significant.

Table 3
Mean cover (% ±S.E.) by lifeform in Coupe93 study plots after 1 year. Values are means of 24, 3 m^2 plots per class

Lifeform	DC2		DC3	
	CL	RIL	CL	RIL
Woody pioneers	16 ± 3	20 ± 5	6 ± 2	10 ± 2
Herbs, grasses and sedges	21 ± 4	24 ± 5	31 ± 5	33 ± 5
Vines	8 ± 2	5 ± 1	13 ± 3	12 ± 3
Other	31 ± 5	35 ± 6	9 ± 3	17 ± 3
Total	75 ± 6	84 ± 5	56 ± 6	73 ± 5

Table 4
First-year survival rates and mean 1-year heights of pioneer seedlings planted in Coupe93[a]

Species	Survival (%)		Mean height (cm) ± S.E.	
	CL	RIL	DC2	DC3
D. moluccana	35	27	26 ± 3	20 ± 2
M. gigantea	67	52	18 ± 2	14 ± 1
M. pearsonii	63	35	29 ± 4	24 ± 3
N. longipedunculata	78	62	14 ± 1	13 ± 2
O. sumatrana	74	50	32 ± 5	31 ± 3

[a] Survival rates did not differ between soil disturbance classes and are pooled across both levels. Heights did not differ between logging systems and are pooled across both levels.

4.1.6. Planted seedlings

Many of the planted pioneer seedlings died during the first year, and few of the survivors thrived (Table 4). Seedling survivorship was greater in CL plots than in RIL plots (LR $\chi^2 = 17.15, \text{d.f.} = 1, P < 0.0001$ in logistic regression), but did not differ between soil disturbance classes ($P = 0.11$) or among blocks within logging systems ($P = 0.29$). In contrast, 1-year seedling heights differed among blocks within logging systems ($F = 4.59, \text{d.f.} = 4, P = 0.0014$ in ANOVA) and were greater in DC2 than in DC3 areas ($F = 4.70, \text{d.f.} = 1, P = 0.031$), but did not differ between logging systems ($P = 0.73$). No interaction term was significant.

4.2. Pioneer demography

The fates of 904 naturally established seedlings were recorded in Coupe91 (Table 5), including 12 pioneer taxa with more than 10 individuals that reached 50 cm height. Tagged seedlings were not uniformly distributed among blocks (LR $\chi^2 = 329.0, \text{d.f.} = 33, P < 0.0001$) and were more numerous in gaps than in skids (LR $\chi^2 = 70, \text{d.f.} = 11, P < 0.0001$). The block by habitat interaction also was significant (LR $\chi^2 = 59, \text{d.f.} = 33, P = 0.0037$). Across all blocks, individual species differed in abundance between gaps and skids (Table 5). *Neolamarckia cadamba* was much more abundant in skids than in gaps, and a similar trend was seen for *D. moluccana* ($P = 0.07$). *Mallotus macrostachys* and *M. indistincta* showed the reverse pattern, with higher abundances in gaps than in skids. Abundances of other species were similar between gaps and skids.

One-year seedling heights differed among blocks ($F = 21.9, \text{d.f.} = 3, P < 0.0001$), among species ($F = 34.2, \text{d.f.} = 11, P < 0.0001$), and between habitat types ($F = 16.7, \text{d.f.} = 1, P < 0.0001$; Table 5). Most of the largest seedlings were *N. cadamba*, *M. macrostachys*, or *Macaranga pearsonii* (Table 5).

Table 5
Number of pioneer tree seedlings by habitat in the Coupe91 demography study, numbers and percentages surviving 1 year, and their heights at 1 year[a]

Species	Total counts		1-Year height (cm) ± S.E.		Surviving 42 months	
	Gap	Skid	Gap	Skid	Number	Percent
D. moluccana	1	11	76	67 ± 8	4	33
Endospermum peltatum	6	5	201 ± 53	74 ± 13	3	27
M. gigantea	14	9	255 ± 38	86 ± 22	8	35
Macaranga hypoleuca	63	51	86 ± 7	68 ± 4	3	3
M. indistincta	17	1	75 ± 12	43	12	67
M. pearsonii	29	23	268 ± 28	149 ± 28	8	15
M. winkleri	36	49	109 ± 9	83 ± 9	0	0
Melicope spp.	3	7	119 ± 31	117 ± 24	1	10
M. macrostachys	27	7	260 ± 28	188 ± 55	15	44
Neonauclea spp.	4	12	106 ± 31	86 ± 16	5	31
N. cadamba	55	459	218 ± 16	189 ± 5	6	1
O. sumatrana	8	7	227 ± 41	127 ± 27	6	40
Total or mean	263	641	170 ± 8	158 ± 4	71	8

[a] Survival did not differ between habitat types and was pooled across habitats. All variables are pooled across replicate blocks.

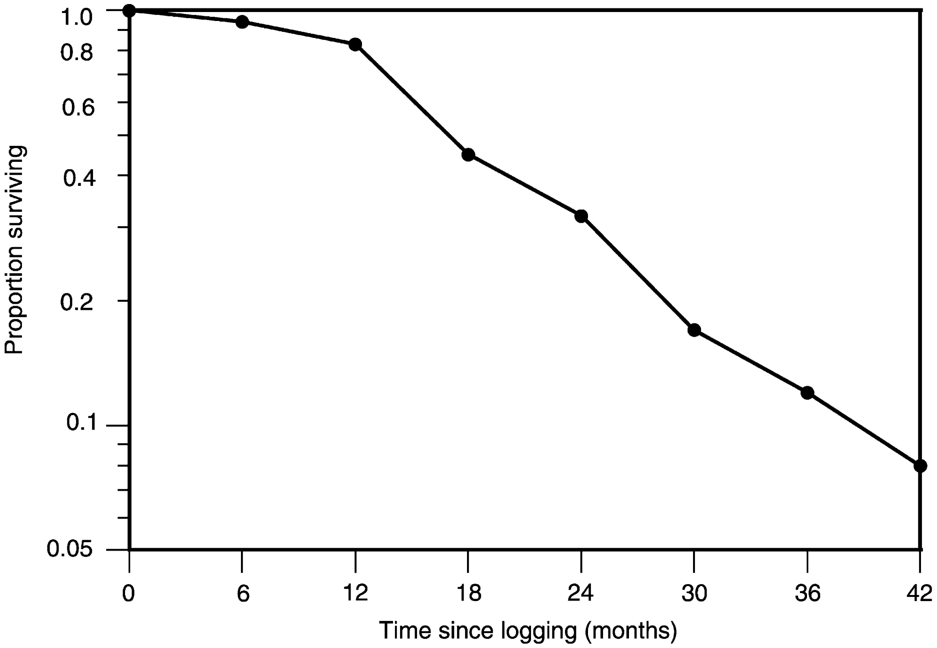

Fig. 1. Survivorship of naturally established woody pioneer saplings in Coupe91, pooled across species, habitats, and blocks.

Over all species, seedlings in gaps averaged 40% taller than did seedlings on skids.

Mortality rates were high; calculated over all species, fewer than 10% of established pioneer seedlings survived for 42 months (Table 5). Although pioneer seedlings more than 50 cm tall experienced only 17% mortality during the first year, mortality rates exceeded 60% per year in the second, third, and fourth year. At the 18-month and 30-month censuses, following the second and third dry seasons experienced by the pioneer colonists, we observed more than 40% mortality (Fig. 1). Survival rates (proportional hazards model: LR $\chi^2 = 261.6, \text{d.f.} = 18, P < 0.0001$) differed among species (LR $\chi^2 = 153, \text{d.f.} = 11, P < 0.0001$), marginally among blocks (LR $\chi^2 = 7.3$, $\text{d.f.} = 3, P = 0.062$) but not between habitat types ($P = 0.67$). Across species, mortality ranged from 100% in *M. winkleri* to 33% in *M. indistincta* (Table 5).

4.3. *Effect of vertebrate herbivores on colonization by woody pioneers*

Some exclosures were damaged by treefalls and animal activities. Elephants destroyed one plot after only 2 months. Two other exclosures also were damaged by elephants but were repaired and retained, since the pioneers inside showed no evidence of browsing. Soon after the 1-year census, elephants destroyed several additional exclosures. Given the consequent reduction in sample size, we analyzed seedling growth for 1 year only. For seedlings in damaged exclosures, survival times were censored at the time damage was observed.

Abundances of woody pioneers differed significantly among replicates (LR $\chi^2 = 137.8, \text{d.f.} = 30$, $P < 0.0001$) and between soil disturbance classes (LR $\chi^2 = 13.0, \text{d.f.} = 6, P = 0.044$), but did not differ between exclosure treatments ($P = 0.36$). More than twice as many seedlings established in DC2 areas as in DC3 areas (Table 6). A significant exclosure treatment by soil disturbance class interaction (LR $\chi^2 = 20.1, \text{d.f.} = 6, P = 0.0027$) reflected relatively large populations of *Macaranga gigantea* seedlings and relatively small populations of *N. cadamba* seedlings on skid tracks in exclosures (Table 6).

First-year seedling heights differed significantly among replicate plots ($F = 5.7, \text{d.f.} = 18, P < 0.0001$), among plant groups in Table 6 ($F = 9.8, \text{d.f.} = 6$, $P < 0.0001$), and between exclosure treatments ($F = 6.9, \text{d.f.} = 1, P = 0.016$), but did not differ between

Table 6
Seedling counts by category of woody pioneers, mean 1-year heights, and percent survival at 21 months for pioneer seedlings inside exclosures and open controls (Coupe92)

Taxon	DC2 (skid edge)						DC3 (skid track)					
	Open plot			Exclosure			Open plot			Exclosure		
	N	Mean height	Survival (%)	*N*	Mean height	Survival (%)	*N*	Mean height	Survival (%)	*N*	Mean height	Survival (%)
Ficus spp.	11	74 ± 20	27	5	117 ± 39	100	6	49 ± 9	17	9	110 ± 33	33
M. gigantea	36	189 ± 17	82	25	197 ± 23	88	7	108 ± 21	24	16	207 ± 31	94
M. hypoleuca	33	50 ± 7	20	34	129 ± 15	63	15	28 ± 6	24	19	94 ± 19	92
M. winkleri	23	66 ± 15	10	23	108 ± 19	91	7	42 ± 18	24	5	164 ± 35	80
N. cadamba	27	41 ± 30	0	40	116 ± 16	16	23	25 ± 5	23	9	49 ± 23	39
Other shrubs	14	140 ± 16	34	9	148 ± 35	89	7	162 ± 35	21	2		0
Other trees	20	95 ± 26	32	13	192 ± 41	65	9	201 ± 45	52	14	92 ± 17	75
Total *N* or mean	164	107 ± 9	34	149	140 ± 9	59	74	79 ± 13	21	74	124 ± 13	72

soil disturbance classes ($P = 0.45$). On average, pioneer seedlings grew 44% taller within exclosures.

Seedling survivorship differed among plots (LR $\chi^2 = 20.6, \text{d.f.} = 5, P = 0.001$), among plant groups (LR $\chi^2 = 98.1, \text{d.f.} = 6, P < 0.0001$), and between exclosure treatments (LR $\chi^2 = 24.0, \text{d.f.} = 1,\ P < 0.0001$), but did not differ between soil disturbance classes ($P = 0.27$; Table 6). Comparing the extremes among the common species, mortality risk for *N. cadamba* was approximately 12 times that of *M. gigantea*. Over all pioneer groups, those in open plots sustained about 1.5 times the mortality of plants in exclosures (Fig. 2). Although this contrast was about twice as great on skid tracks as on skid edges,

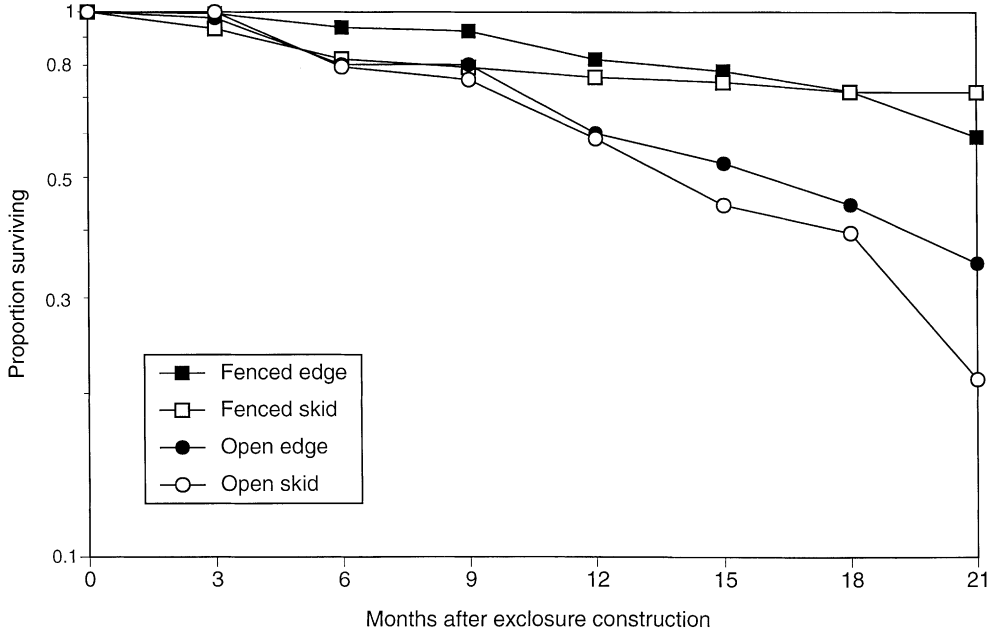

Fig. 2. Survivorship of pooled woody pioneer seedlings in Coupe92, compared between exclosures and open controls and between two soil disturbance class.

interaction of soil disturbance class with exclosure treatment was not significant.

5. Discussion

Woody pioneers have just a short window of opportunity in which to colonize disturbances that are unpredictable in both space and time. Successful recruitment into these ephemeral sites depends both on seed delivery, especially in early successional habitats (Turnbull et al., 2000), and on site conditions conducive to seedling growth and survival. In addition, herbivory impairs plant performances, and its effects may vary with site conditions. In the lowland rain forests of eastern Borneo, low seed availabilities, high seedling mortality due to unfavorable site characteristics, and herbivory all limit recruitment and can contribute to spatial heterogeneity in the distributions of woody pioneers across post-logging habitats.

5.1. Contributions of seed availability to pioneer patchiness

As in other recent disturbances within mature tropical forests (Garwood, 1989; Saulei and Swaine, 1988; Dupuy and Chazdon, 1998), pioneer seed and seedling abundances were low and patchy at our logged sites. The vast majority of most species' seeds were collected in just a few seed bank or seed rain samples (see also Butler and Chazdon, 1998). Instead of pioneer trees, *Uncaria*, a wind-dispersed liana that can develop dense vine tangles in logged forests (Putz, 1985), was the most abundant seed bank taxon (see also Kennedy and Swaine, 1992). Both seed and seedling populations were greater in topsoil-exposed (DC2) areas than in subsoil-exposed (DC3) areas. Because seed banks are concentrated in the upper soil layers (Garwood, 1989), removal of litter and topsoil would have removed a portion of the seed bank, and also may have allowed greater erosion loss of later arriving seeds. Soil disturbance did not affect seed rain, which thus assumed greater relative importance with increased disturbance. In both the Coupe93 seed availability trials and the Coupe92 exclosure experiment, DC3 areas supported fewer pioneer seedlings than did DC2 areas, and a similar pattern was observed between gaps and skids in Coupe91. Even where unfavorable site conditions also reduced seedling survival (see below), insufficient seed availability, coupled with low rates of establishment from the seed bank (e.g., the 2.5% measured by Kennedy and Swaine (1992)), could have limited pioneer colonization of disturbed sites.

Seed addition increased seedling populations of four *Macaranga* species as well as *Duabanga*, indicating some limitation of pioneer recruitment by seed availability at least through the end of the first year. In contrast, an earlier study in Coupe91 found that site conditions were more important than was seed availability in determining the sizes of pioneer sapling populations at 1 year. Different short-term consequences of seed addition may reflect seasonal, annual, or spatial variation in seed abundances. Both seasonal and annual variation in seed availability (e.g., Dalling et al., 1997; Dupuy and Chazdon, 1998) can produce substantial variation in recruitment (e.g., Schupp, 1990). Many southeast Asian pioneer species fruit seasonally (Davies and Ashton, 1999), and seed banks as well as seed rain must fluctuate as a result. We sampled seed banks before peak seed production by *N. cadamba* and most species of *Macaranga*, and small observed seed banks may reflect seasonal minima. In contrast to observations in Sarawak (Davies and Ashton, 1999), many individuals of *Macaranga* species at DVFC did not fruit in 1993 (B.E. Howlett, unpublished data), and few seeds arrived in the seed rain during the monitoring period. *Octomeles* did not respond to seed addition, but mature *Octomeles* trees were abundant in Coupe93 and produced large fruit crops in July–August 1993, contributing their tiny, wind-dispersed seeds to most study plots. Because the timing of logging is random with respect to the annual and super-annual reproductive phenologies of particular plant species, it may contribute to the considerable spatial variation in the composition of subsequent pioneer communities. Particularly in Asian primary rain forests, which have relatively few natural disturbances and low densities of *Macaranga* and other pioneer trees (Putz and Appanah, 1987; Primack and Lee, 1991; but see Davies et al., 1998), low and variable seed populations might often constrain pioneer colonization after logging.

5.2. Contributions of site conditions to pioneer patchiness

Differences in pioneer establishment across blocks and between soil disturbance classes demonstrate the importance of site factors in determining the relative abundances of various pioneer taxa. Because recruitment in Coupe91 was not limited by seed availability after 6 months (Pinard et al., 1996), observed among-block differences in pioneer sapling populations could reflect responses to intrinsic site characteristics. Across all experiments, vehicular traffic caused degraded soil conditions that decreased pioneer colonization. Subsoil-exposed plots on skid tracks exhibited greater soil strengths and bulk densities (Nussbaum, 1995) than did topsoil-exposed plots, and compaction, aggravated by topsoil removal, restricts plant access to water and nutrients (Nussbaum et al., 1995). These conditions were associated with reduced vegetative cover and with the dominance of herbs, grasses and sedges over woody pioneers (see also Pinard et al., 2000). In the Coupe92 herbivory experiment, pioneers were twice as abundant on skid edges (DC2) as on the skid tracks (DC3). For the majority of species in Coupe91, the number of pioneers in gaps exceeded those on skid tracks (Table 5). Similarly, in Costa Rica, Guariaguata and Dupuy (1997) found greater colonization at the edges of skid tracks than in their centers, as well as a long-term reduction in community diversity in the skid centers. Pinard et al. (2000) showed that abandoned skid tracks in Sabah were impoverished in small woody stems even 18 years after logging. Such observations suggest that site factors, along with seed availability, affect species' distributions and abundances.

In addition to reducing seedling colonization, soil compaction and nutrient depletion associated with topsoil removal may reduce pioneer performances. For both planted (Coupe93) and established (Coupe91) seedlings, 1-year heights on topsoil-exposed areas exceeded those subsoil-exposed areas. However, despite generally high mortality rates for both natural and planted seedlings, first-year mortality rates did not differ across soil disturbance classes (Coupes 91, 92, 93). Once established, seedlings may be more resistant to the effects of topsoil removal than are germinating seedlings, even though reduced growth rates in poor sites may accumulate to increase mortality over longer time periods. For *Macaranga* species, among the best survivors in our studies, our records showed higher sapling mortality rates than Davies (2001) reported for *Macaranga* trees in Sarawak, but they support his observation that mortality rates decreased and growth rates increased with size. Seedling mortality does increase in the most disturbed sites, such as log yarding areas, where serious nutrient deficiencies result in slow growth and high mortality for planted seedlings of both pioneer and dipterocarp species (Nussbaum et al., 1995; B.E. Howlett, unpublished data). Heil et al. (2001) showed that nutrient availability for *Macaranga* host plants affects the numbers and activities of their resident ant colonies, and so nutrient-limited plants may suffer greater herbivory. In sum, while subsoil exposure and compaction reduce both seedling survival and growth, less severe disturbance affects pioneer growth rates more than (short-term) survival.

5.3. Effects of vertebrate herbivores on woody pioneers

Mammalian herbivory impeded development of tropical pioneer communities after logging. Exposure to herbivores reduced pioneer growth rates by an average of 44% and more than doubled seedling mortality. Differentially high herbivory on control plots may have moderated after 1 year, since many of the surviving pioneer saplings exceeded 3 m in height and were out of reach of most terrestrial browsers. However, slower growth rates on skid tracks left seedlings vulnerable to herbivore damage for a longer time period. Interspecific interactions also may affect individual species responses to site conditions and herbivory. For *M. gigantea* and to a lesser extent *M. hypoleuca*, herbivore exclusion on skid tracks more strongly affected both survivorship and growth than it did on skid edges, probably due to the reduced nutrient availabilities to support compensatory growth in the former habitat. In contrast, differential survivorship of *N. cadamba* in exclosures was more pronounced on skid edges than in skid tracks, possibly because, in the former (more favorable) habitat, competition from the *Macaranga* species compounded the effects of herbivory. The degree to which preferential grazing and browsing of early successional species slows succession in recovering rain forests should depend on the relative strengths of herbivory vs. other sources of seedling and sapling mortality, which is high even in the absence of herbivory. Nevertheless, since herbivore densities tend to be higher in pioneer forests than in adjacent primary forests (Grieser Johns, 1997, for sambar deer, elephants and macaques), herbivory may often hinder the establishment of pioneer forests. To safeguard populations of palatable pioneer species, limited reductions in these unnaturally high herbivore populations might be warranted, particularly in regions where conventional logging has left relatively large areas of degraded soils (Pinard et al., 2000) that interfere with the capacities of pioneer species to outgrow herbivory.

5.4. Effects of logging system on pioneer establishment

Logging system did not affect soil strength within either soil disturbance class, but it significantly influenced the extent of soil disturbance as well as canopy cover. Although the same type of disturbances occur in both RIL and CL, the relative areas differ significantly between logging systems. Pinard et al. (2000) found that roads and skid tracks covered 17% of a CL area, compared with just 6% of the RIL area. In addition, RIL skid tracks received less soil disturbance than did CL skids (Pinard et al., 2000), reducing the extent of severely disturbed sites resistant to pioneer colonization. Despite lower seed rain under RIL, shrubs and treelets established at higher densities in RIL than in CL, and topsoil-exposed areas supported more pioneers in RIL than in CL. This discrepancy suggests that conditions for seedling establishment were better after RIL, perhaps because of lesser soil disturbance or because greater canopy cover by remnant vegetation ameliorated water stress for seedlings recruiting in disturbed areas. Growth of planted seedlings did not differ by logging system, but lower seedling survivorship in RIL than in CL blocks may also result from the greater vegetative cover. Regardless, by limiting soil and canopy degradation during logging operations, adoption of RIL practices should promote subsequent recovery.

Although colonization by pioneers (“belukar”) after logging may be viewed unfavorably, pioneers do not necessarily compete with more desirable species (Pinard et al., 1998), and may even provide satisfactory “nurse-plant” canopies under which persistent species can thrive (Brown and Lugo, 1990; Montgomery and Chazdon, 2002). Pioneer stands can provide a structure and microclimate resembling that of natural forest, but with higher light levels (Howlett, 1998). Moreover, the production of short-lived pioneer leaves provides an organic substrate for nitrogen fixation and should contribute to the nitrogen economies of forests recovering from logging. Given these potential benefits of pioneer cover and the observation that pioneer forests tend to regenerate unevenly across the post-logging landscape, the promotion of pioneer tree recruitment might be advisable. Although seed availabilities limited pioneer recruitment in our study, and strategies to increase seed availability might favor pioneer forests, widespread seeding may be impractical. Site conditions also greatly influence the success of pioneer recruitment, and logging practices can be managed to promote better post-logging conditions.

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