

independently. We labeled one sample with Cy3 and the other with Cy5, then hybridized both samples to the same array. The mean normalized ratio of Cy3: Cy5 signal intensity for more than 3500 genes was 0.996 with a SD of 17.6% of the mean and a SE of 0.003. Few genes fluctuated greater than 2.0-fold and no genes on the array appeared to be differentially expressed more than 2.5-fold in this single experiment. Each value in our data set represents the average of replicate experiments. Therefore, we consider a threefold differential to be a conservative criterion for gene selection. Five hundred and sixty genes exhibited a threefold or greater differential relative to PF. Twenty-six of these genes were then culled from this set because of a lack of reproducibility, usually due to signal that was below threshold (leaving 534 genes). The threshold was set at a signal intensity of 1000. The value of 1000 is typically between 2 and 3 SDs above the mean background value in these microarray experiments.

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Impact of El Niño and Logging on Canopy Tree Recruitment in Borneo

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Dipterocarpaceae, the dominant family of Bornean canopy trees, display the unusual reproductive strategy of strict interspecific mast-fruiting. During 1986–99, more than 50 dipterocarp species dispersed seed only within a 1- to 2-month period every 3 to 4 years during El Niño–Southern Oscillation events. Synchronous seed production occurred across extensive areas and was essential for satiating seed predators. Logging of dipterocarps reduced the extent and intensity of these reproductive episodes and exacerbated local El Niño conditions. Viable seed and seedling establishment have declined as a result of climate, logging, and predators. Since 1991, dipterocarps have experienced recruitment failure within a national park, now surrounded by logged forest.

Global climatic cycles, such as El Niño–Southern Oscillations (ENSO), affect diverse ecological processes including community dynamics and landscape disturbances in tropical regions (1). Dipterocarpaceae, a monophyletic group of trees (2), dominate low- to mid-elevation tropical forests in Southeast Asia and can contribute $\geq 70\%$ of canopy biomass (3, 4). Of the 257 species on the island of Borneo, most are insect-pollinated, obligate outcrossers that flower asynchronously on supra-annual cycles (5). Dipterocarps produce single-seeded fruits; are dispersed by wind, water, or gravity; and germinate within days of dispersal. Primary

or secondary dispersal agents have not been documented (4, 6).

Mast-fruiting, the supra-annual production of large seed crops interspersed by irregular periods of low seed production, has been challenged as a distinct biological phenomenon (7). Therefore, the geographic, taxonomic, and temporal extent of synchronous reproduction in plants must be quantified to address these claims (7, 8). Our 14-year investigation tests assertions that Bornean dipterocarps display mast-fruiting over large spatial scales (9). Five dipterocarp genera and 54 sympatric dipterocarp species were monitored for fruit production, seed damage, and seedling establishment (10) across two watersheds (15 km²) within Gunung Palung National Park (GPNP; 90,000 ha), West Kalimantan (146,760 km²; Indonesian Borneo).

To assess the logging impact on dipterocarp recruitment across West Kalimantan, we also conducted 3 years of field research within 12 logging concessions, compiled a decade of logging records across all 72 timber concessions, collected dipterocarp seed export data covering a 30-year period, digitized land use maps, and assessed Landsat TM images of the GPNP region from 1988 to 1998.

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These data were combined with 30 years of global and regional climatic data to examine the effects of ENSO cycles on dipterocarp seed production. The Multivariate ENSO Index (MEI) is based on six climatic variables recorded over the tropical Pacific (sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky) (11).

From 1986 to 1999, four reproductive episodes were detected with an average inter-mast interval of 3.7 years (± 0.3 ; annual coefficient of variation = 222%) (Fig. 1A). All fruiting episodes, with the possible exception of one extremely minor event in 1994, occurred during ENSO years. Seed export records from 1969 to 1999 document that periods of high dipterocarp seed production across West Kalimantan also were correlated with ENSO years ($P = 0.024$) (Fig. 1B). Our field surveys confirm that dipterocarp fruit production may occur synchronously across much of this region during ENSO (4). Significantly greater seed exports in ENSO versus non-ENSO years ($P = 0.006$) document the spatial scale of mast events and confirm the periodicity of seed production (3.0 ± 0.3 to 5.2 ± 1.0 years) monitored in the park (Fig. 1A). A similar 3.5- to 5.6-year climatic periodicity corresponding to ENSO has also been documented with 272 years of dendroclimatic reconstruction by using Indonesian teak growth rings (12). Synchronous reproduction across this region occurs on irregular 3- to 6-year intervals.

Climatic conditions associated with ENSO provide an irregular supra-annual, regional cue initiating asynchronous, widespread flowering in Bornean Dipterocarpaceae. In West Kalimantan, the onset of ENSO cycles is marked by an extreme reduction in June to September rainfall, and the MEI (11) in these months preceding flowering is positively correlated with seed production ($P = 0.04$; 10,000 permutations). However, a composite MEI value, over the full 5-month flowering and fruit maturation period (September through February), best predicts the magnitude of dipterocarp seed production from 1969 to 1997 ($P = 0.012$, 10,000 permutations) (Fig. 1B). Thus, ENSO conditions not only trigger dipterocarp flowering, but ENSO characteristics appear to influence regional seed production and recruitment.

Within the 15-km² area sampled, nearly every dipterocarp species that was distributed over a variety of bedrock materials, and two watersheds, produced seed in each major event (for example, 1991) (Fig. 2, A to D). Forty-eight sympatric dipterocarp species in five genera, and 80 to 93% of all dipterocarp individuals [>49 -cm diameter at breast height (DBH)] spanning an elevational gradient [15 to 1000 m above sea level (asl)],

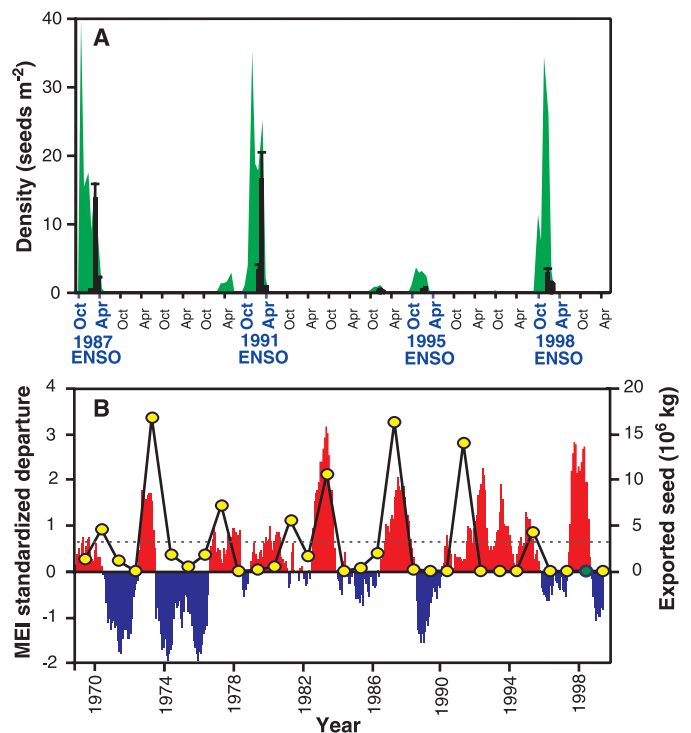
participated in the 1987 and 1991 mast events (4). Over 94% of all viable seed fell in 6 weeks in each of the five reproductive episodes (Fig. 1A). In 1987 and 1991, lowland viable seedfall was 25 to 30 kg ha⁻¹ week⁻¹ (dry mass) with viable seed production for each mast event reaching 155.9 kg ha⁻¹ (± 37.2) and 195.9 kg ha⁻¹ (± 30.9), respectively. For all other years combined, viable seed production averaged only 3.3 kg ha⁻¹ year⁻¹ (± 2.1 ; $n = 11$). Canopy tree seed production was limited to these supra-annual events. This system, with temporally concentrated fruitfall, broad species participation, and widespread geographic involvement, is the only documented case of "strict interspecific masting" (13, 14).

Of the several hypotheses to explain plant reproductive synchrony (7-9, 13-16), seed-predator satiation appears to be a major factor maintaining synchronous seedfall in the Bornean Dipterocarpaceae (13). Pre- and postdispersal seed predation by invertebrate and vertebrate seed predators impart the selective force that may explain the maintenance of synchronous fruitfall across taxa and regions (4, 6). Several nomadic vertebrates (4) and ≥ 25 insect species (17) depend on dipterocarp seed for growth and reproduction. Seedling establishment is a major bot-

tleneck in dipterocarp recruitment (6). In minor or localized fruiting events, seed predators destroy a significantly greater proportion of seeds than in major regional events (4). Regional synchronous seed production is critical for this reproductive strategy to be successful; nomadic seed predators move across the landscape to feed on dipterocarp seed (4, 6). Predator satiation occurs across the landscape rather than within a local site (4, 6), but otherwise conforms to Janzen's predator-satiation hypothesis (9, 16). Without sufficient quantity and spatial extent of seed production, vertebrates may concentrate in specific areas and can destroy all seed produced in a local stand (4).

Given the spatiotemporal scale of this interspecific mast-fruiting and the dynamics of seed predators, commercial logging is expected to have both direct and indirect effects on the mast-fruiting dipterocarp landscape. These effects may occur at the logging concession and in nonlogged, protected forests. Current logging practices may disrupt the dipterocarp reproductive response, and thus seedling recruitment, in at least three ways: by (i) reducing the local density and biomass of mature trees, (ii) reducing the spatial extent of participation in a mast, and (iii) altering responsiveness to ENSO by disrupting

Fig. 1. Dipterocarp fruitfall and ENSO events. **(A)** Total monthly fruitfall (green) of all seed with viable or undamaged ripe seed (black) per square meter (mean \pm SEM) arriving in traps (73.4 m²) monitored over 150 months. ENSO years are indicated in blue. Viable seed (26 dipterocarp spp; five genera) was present during 40 (6.2%) of the 644 weeks. **(B)** Regional dipterocarp seed exports were correlated with the Multivariate ENSO Index (MEI). MEI is based on six climatic variables recorded over the tropical Pacific (11). The MEI is calculated as the first unrotated principal component of all six observed fields combined and computed separately for each bimonthly period (December-January, January-February, ...). Red bars indicate ENSO years, blue bars indicate La Niña events, and yellow circles depict seed export levels (hatched line is mean seed production for all years). Dipterocarp seed export records were compiled from forestry archives. Differences between ENSO (5.06×10^6 kg) and non-ENSO (0.72×10^6 kg) mean seed production levels were significant ($P = 0.007$ in 10,000 permutations). ENSO years are counted conservatively as both years in a sequence. Seed production greater than the mean across all 31 years ($>2.96 \times 10^6$ kg) occurred in 8 years, of which 7 years were associated with ENSO events ($P = 0.024$ in 10,000 permutations). The 1998 value (green circle) is excluded from MEI calculations because the seed market crashed (0.16×10^6 kg).



edaphic conditions or causing extended drought stress.

Dipterocarps contribute over 85% of Indonesia's timber exports, generating as much as U.S. \$6 billion in annual export revenue, and Kalimantan provided ~60% of Indonesia's exports (18, 19). From 1987 to 1997, West Kalimantan logging concessions delivered 22.4×10^6 m³ of logs to industries [(3.6 to 1.7) $\times 10^6$ m³ year⁻¹]. The 36 mechanized concessions surveyed transported a mean of 54.3 m³ ha⁻¹ year⁻¹ (± 2.7) of logs (taxed at the mill) and dipterocarps were 88 to 96% of production volume (19). Other Bornean sites report similar extraction levels (87 to 104 m³ ha⁻¹), with only ~40 to 55% of actual felled volumes recorded at the mill (20). This intense logging has greatly reduced the regeneration capacity of dipterocarp forests.

Uncontrolled logging has destroyed most reproductive dipterocarps in harvested stands. Though forestry regulations permit 56 to 72% of commercial standing volume (reported by the company) to be harvested, the 12 timber companies observed on-site logged any healthy, accessible dipterocarp adult in felling blocks (19). In a pre- and postlogging experiment, we monitored dipterocarp reproduction in a logging concession during the 1991 mast-fruited (21). This site was harvested 1 year later. Fifteen dipterocarp trees per hectare (basal area 8.0 m² ha⁻¹) were felled, and an additional 7.5 trees ha⁻¹ (4.4 m² ha⁻¹) were damaged, killed, or defective. Only 0.8 trees ha⁻¹ of undamaged reproductive dipterocarps (3%) remained (21). To determine the longer term potential for dipterocarp regeneration after logging, we conducted a separate study throughout a 100-ha area that was logged 8 years before the 1991 mast-fruited (6, 22). Even with 8 years to recover from logging, few dipterocarp trees were reproductive in 1991 (5.8 trees ha⁻¹; 2.2 m² ha⁻¹ or an 83% reduction from preharvest control levels: 25.5 trees ha⁻¹; 13.0 m² ha⁻¹) (6). Dipterocarp seedling production was only 15% of the unlogged control. Thus, logging has considerably reduced dipterocarp seed production and regeneration in logged-over forests for at least a decade.

Logging has fragmented a once-contiguous expanse of dipterocarp forest and thus disrupted regional reproductive response during mast events. From 1968 to 1998, 72 timber concessions once occupied as much as 79.2% (7.3 $\times 10^6$ ha) of West Kalimantan's forested land. The average area of a mechanized operation was 111,319 ha (± 8883) (19). During their lease, companies harvest 57% of the forested area in a patchwork of felling sites distributed throughout the concession (19). Subtracting highly degraded areas (roads, log yards, and camps), fully 77 to 87% of the area is affected (19). Most importantly, since 1992, licenses have been granted

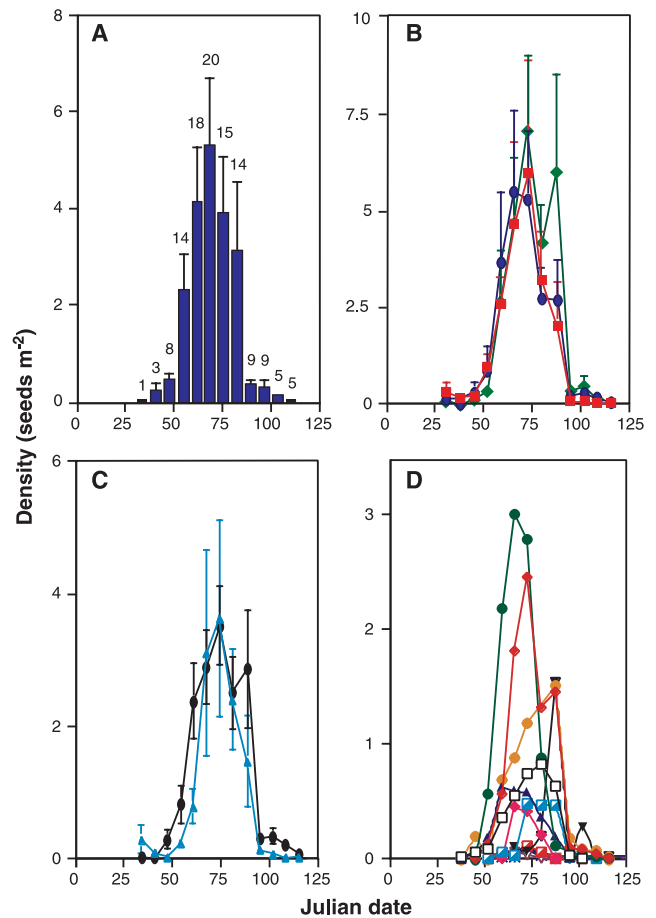
to establish plantations of nonnative monocultures in 1.2 $\times 10^6$ ha of logged or secondary forests (19). Forest conversion has occurred without regional planning and has created a mosaic of degraded, logged-over areas and nonnative monocultures surrounding protected areas including GPNP.

Although the ENSO-associated conditions that influence dipterocarp fruit production remain ambiguous (23), changes in rainfall and local climate are expected to affect their phenology, seed production, and seedling establishment. The severity of ENSO-associated droughts has increased significantly in West Kalimantan over the past two decades ($P < 0.05$), even excluding the intense 1997–98 ENSO (24). Reduced rainfall inception and moisture-retention capacity have been documented in these logged forests (25) and may exacerbate the local impact of sharp declines in regional rainfall during ENSO (24). In West Kalimantan, catastrophic droughts coupled with large-scale, anthropogenic forest fires have been recorded in every ENSO event since 1991 after intensive logging and

especially since plantation clearing began (24, 26). Moreover, at least 80% of the 1997–98 ENSO-associated fires across Indonesia (primarily Kalimantan) were caused by logging and plantation firms (18). Thus, logging and associated plantations appear to influence local ENSO conditions.

Logging has reduced the spatial participation and intensity of masting through its effects on regional dipterocarp density, distribution, seed production, and climatic conditions and, as a result, has influenced dipterocarp reproductive synchrony and seedling recruitment elsewhere—even within GPNP. After the 1991 mast, 42.3 and 61.5% of dipterocarp species initiated fruit production in 1994 and 1995, respectively, but only 0.8 and 2.3% of initial fruit production was viable. Both values are significantly lower than either the 1987 or the 1991 mast ($P < 0.0001$) (Fig. 1A). The 1990–95 ENSO was possibly the longest on record (27) (Fig. 1B). Thus, dipterocarp seed production may have been altered, triggering two minor consecutive events in 1994 and 1995. Then a major

Fig. 2. Synchrony of dipterocarp fruitfall across various scales in 1991. Traps (146.9 m²) were sampled weekly. (A) Total lowland seed production (mean \pm SEM week⁻¹). All 26 lowland dipterocarp species that reach adult size in mid-story, canopy, or emergent strata produced seed. Numbers of species arriving in traps are indicated above bars. (B) Production in three lowland habitats with distinctive dipterocarp communities (mean \pm SEM week⁻¹): (■) alluvium 15 to 50 m asl; (◆) sedimentary 50 to 150 m asl; (●) granite 150 to 300 m asl. All pairwise cross-correlation comparisons were maximally correlated with a lag of zero weeks (each $r \geq 0.895$, each Bonferroni $P \leq 0.002$ in 10,000 permutations). (C) Production in two watersheds (mean \pm SEM week⁻¹). Seedfall was maximally correlated with a lag of zero weeks (cross-correlation $r = 0.972 \pm 0.277$, $P < 0.0001$ in 10,000 permutations). (D) Production by the 11 most abundant species (mean week⁻¹). Species' seed dry mass range 0.15 to 6.0 g. Seedfall measures were maximally cross-correlated at a mean lag of 0.07 ± 0.17 weeks. Of the 55 comparisons, 19 were maximally correlated with a lag of zero weeks, 11 of which were significant (each Bonferroni $P \leq 0.0009$); 43 comparisons were maximally correlated within a 1-week lag, 21 of which were significant. The least-synchronous of these 11 species, *Shorea gibbosa* Brandis (▼), demonstrated a mean lag to other species of only 1.9 weeks.



fruiting event occurred in 1998. Given the lapse in substantial fruit production, we expected the 1998 mast to produce large seed crops. Although 73% of dipterocarp species attempted to mature fruit, viable seed was significantly lower than in 1987 and in 1991 ($P = 0.0018$ and $P = 0.0003$, respectively) (Fig. 1A). Catastrophic drought and smoke from nearby forest fires may have contributed to this off-site reduction in productivity through a combination of factors including pollination failure and water and nutrient stress. Across West Kalimantan, seed exports also were greatly reduced in 1995 and almost failed completely in 1998—indicating potential large-scale, synergistic impacts of ENSO, logging, and plantations (Fig. 1B).

A decade of dipterocarp logging and plantation conversion in Kalimantan has reduced protected forests to islands of relatively high seed density. Over 2×10^5 ha of forest surrounding GPNP have been degraded by

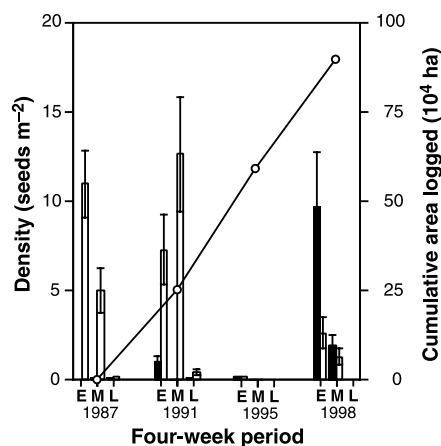


Fig. 3. Vertebrate seed predation (black bars) increased and viable seed production (white bars) decreased across four mast events with increasing logged area (○). Seed density is subdivided into three (4-week) periods (E, early; M, middle; and L, late) for 1987, 1991, 1995, and 1998. Cumulative area logged (10^4 ha) is summed from forestry department's concession records for 1987–91, 1991–95, and 1995–99 and includes some permits granted for logging before plantation clearing. Peak seedfall had significantly lower seed predation than in tails of the fruitfall distribution in 1987 and 1991 ($P = 0.0001$ in 10,000 permutations). Seed production and amounts of seed destroyed by vertebrates differed significantly among years ($P = 0.004$ and $P = 0.005$, respectively; repeated measures analysis of variance). The 1998 event had significantly lower total seed production than 1987, $P = 0.0003$, or 1991, $P = 0.0018$, and greater total seed predation than 1987, $P = 0.0003$, and 1991, $P = 0.0105$ (Bonferroni-transformed significance values determined from 10,000 permutations constraining repeated sites). Neither 1987 nor 1991 differed in total seed production ($P = 1.000$) or predation ($P = 0.198$). In 1998, timing of seed predation in the last 2 weeks was reconstructed from seed traits because collection was delayed.

logging, plantations, and fire in 1994–95 and 1997–98. During recent mast-fruiting events, this protected site has become a relatively concentrated source of dipterocarp seed in a matrix of logged forest or nonnative monocultures with marginal dipterocarp seed production. In 1998, vertebrate seed predation was significantly greater than in previous mast events (Fig. 3), reflecting an increase in the local densities of seed predators. Degraded areas probably can no longer support vertebrate seed predators. At GPNP, the timing of vertebrate seed predation also differed from 1987 and 1991, as seed was destroyed throughout seedfall, not just in the tails of the seedfall distribution (Fig. 3). Within GPNP, seed predators had a significant negative impact on seedling production in the 1995 and 1998 mast events.

The proportion of dipterocarp species producing viable seed also was altered. In 1998, only 34.6% of the species produced viable seed and just two species contributed 86.7% of the total production. Despite extensive sampling across large lowland areas in three ecosystems (2430 m^2 across $\sim 3 \text{ km}^2$) (10), 4 months after this fruitfall, new dipterocarp seedlings were not found. This contrasts with $155,824$ dipterocarp seedlings ha^{-1} ($\pm 36,764$) (26 of 26 spp.) recorded in the lowlands 3 months after fruitfall in 1991, at which time $18,941$ seedlings ha^{-1} (± 3866 ; 21 of 26 spp.) had survived from the 1987 mast (4, 6). Given these infrequent reproductive events, a decade of widespread regeneration failure of the dominant canopy trees will alter species' interactions and community dynamics.

That dipterocarp reproductive success is highly correlated with ENSO suggests that the frequency, duration, or intensity of ENSO-associated conditions experienced in this region are critical for dipterocarp recruitment. Land use may either alter ENSO-associated conditions or intensify their local impact (26, 27). Given the spatial scale of mast-fruiting synchrony and necessity for predator satiation, regional logging and especially subsequent conversion to plantations affects Dipterocarpaceae and their seed predators even within a large national park. Dipterocarp populations may respond to altered climatic patterns with more frequent, low fruit production or with asynchronous fruiting, both of which will affect levels of seed predation and viable seed. Alternatively, reproductive failure could result from the inability to satiate seed predators coupled with drought-induced seed or seedling mortality. The long-term dynamics of both dipterocarps and their seed predators remain complex and unstable.

Gunung Palung may be the only national park remaining in Indonesian Borneo that still contains large areas of nondegraded, lowland dipterocarp forest. Despite three

mast-fruiting attempts in 8 years, ≥ 48 species of canopy trees have not produced adequate seedling regeneration since 1991. This reproductive strategy appears particularly vulnerable to disruption. Degradation of dipterocarp forests will have repercussions both in Bornean terrestrial ecosystems and in regional economies with global implications in as yet unforeseen ways.

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- 1.5 × 10⁴ ha or 35.9% of the mechanized production area operating in 1992. Data are compiled from *Rencana Struktur Tata Ruang Propinsi Kalimantan Barat* (BAPPEDA-KALBAR, Pontianak, Indonesia, 1992), vols. 1–5; *Rencana Karya Tahunan Pengusahaan Hutan* (Timber Concessions, Pontianak, Indonesia, 1986–96); *Statistik Kehutanan Tahunan* (Departemen Kehutanan–KALBAR, Pontianak, Indonesia, 1986–99); *Statistik Kehutanan Indonesia* (Departemen Kehutanan, Jakarta, Indonesia, 1986–99); www.dephut.gov.id/utama.asp.
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21. Timber stand was mapped for dipterocarp demography (>19 cm DBH), and fruit production, seed predation, and seedling establishment were monitored during the 1991 mast-fruiting event. This stand was felled by the company's most experienced chainsaw operators following their standard protocol (except that minimum felling size regulations were enforced). This re-census occurred after felling, but before skidding and removal of felled trees, so it includes only felling damage.
22. Means for 20 transects (250 m by 30 m) stratified randomly across a 2 km by 0.5 km (100 ha) compartment logged 8 years before measurement. Only dipterocarps were harvested, and no silvicultural treatments were applied in the compartment. All dipterocarp trees (25 spp., 5 genera, >19 cm DBH) and stumps were measured, identified to species, assessed for fruit in crown, and mapped in the logged area and throughout an adjacent unlogged control area. From 1991 to 1993, seed and seedling production were monitored in 170 (1 m²) plots in the logged area and 50 (1 m²) plots in the unlogged control.
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