19. K. Misawa, N. Nakamura, *Geochim. Cosmochim. Acta* **52**, 1699 (1988).
20. R. H. Jones, T. Lee, H. Conolly, S. G. Love, H. Shang, in *Protostars and Planets IV*, V. Mannings, A. P. Boss, S. S. Russell, Eds. (Univ. of Arizona Press, Tucson, AZ, 2000), pp. 927–962.
21. N. Nakamura, in *Primitive Solar Nebula and Origin of Planets*, H. Oya, Ed. (Terra Scientific, Tokyo, 1993), pp. 409–425.
22. C. M. O'D. Alexander, *Geochim. Cosmochim. Acta* **58**, 3451 (1994).
23. See supporting data on *Science* Online.
24. A. Pack, H. Yurimoto, H. Palme, *Geochim. Cosmochim. Acta*, in press.
25. G. Crozaz, L. L. Lundberg, *Geochim. Cosmochim. Acta* **59**, 3817 (1995).
26. W. Hsu, G. Crozaz, *Geochim. Cosmochim. Acta* **62**, 1993 (1998).
27. A. Krot, B. Fegley, K. Lodders, H. Palme, in *Protostars and Planets IV*, V. Mannings, A. P. Boss, S. S. Russell, Eds. (Univ. of Arizona Press, Tucson, AZ, 2000), pp. 1019–1054.
28. H. Nakano, A. Kouchi, S. Tachibana, A. Tsuchiyama, *Astrophys. J.* **592**, 1252 (2003).
29. Y. Guan, G. R. Huss, G. J. MacPherson, G. J. Wasserburg, *Science* **289**, 1330 (2000).
30. T. J. Fagan, A. N. Krot, K. Keil, *Meteorit. Planet. Sci.* **35**, 771 (2000).
31. G. Kurat, E. Pernicka, I. Herrwerth, *Earth Planet. Sci. Lett.* **68**, 43 (1984).
32. M. E. Varela, G. Kurat, P. Hoppe, F. Brandstätter, *Geochim. Cosmochim. Acta* **66**, 1663 (2002).
33. J. N. Grossman, C. M. O'D. Alexander, A. Brearley, *Meteorit. Planet. Sci.* **37**, 49 (2002).

34. We thank J. Zipfel for loaning thin sections of Dar al Gani 369 and Dar al Gani 378, C. M. Allen for her help and fruitful discussions concerning LA-ICPMS data reduction, and H. St. O'Neill and D. Kelly for their support during the stay of A.P. at Australian National University. Supported by Deutsche Forschungsgemeinschaft grants PA 346/24 1 (H.P.) and PA-909/1-1 (A.P., DFG Emmy Noether-Programm).

Supporting Online Material
www.sciencemag.org/cgi/content/full/303/5660/997/DC1
Materials and Methods
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23 October 2003; accepted 9 January 2004

Lowland Forest Loss in Protected Areas of Indonesian Borneo

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The ecology of Bornean rainforests is driven by El Niño–induced droughts that trigger synchronous fruiting among trees and bursts of faunal reproduction that sustain vertebrate populations. However, many of these species- and carbon-rich ecosystems have been destroyed by logging and conversion, which increasingly threaten protected areas. Our satellite, Geographic Information System, and field-based analyses show that from 1985 to 2001, Kalimantan's protected lowland forests declined by more than 56% (>29,000 square kilometers). Even uninhabited frontier parks are logged to supply international markets. "Protected" forests have become increasingly isolated and deforested and their buffer zones degraded. Preserving the ecological integrity of Kalimantan's rainforests requires immediate transnational management.

Conversion, degradation, and fragmentation threaten the integrity of forested ecosystems worldwide (*1–3*). In Indonesian Borneo (Kalimantan), concession-based timber extraction, plantation establishment, and weak institutions have resulted in highly fragmented and degraded forests (*4*, *5*). In such dynamic tropical rainforest frontiers with high biodiversity (*6*), investigations are required at local to regional scales to understand how changes in land use and land cover alter ecological interactions (*7*, *8*).

Kalimantan's rainforests are driven by El Niño Southern Oscillation events, which trigger synchronous fruiting among the regionally dominant timber trees, the Dipterocarpaceae, and bursts of faunal reproduction (*8–10*). Dipterocarp reproductive cycles are linked to rural livelihoods; communities both trade dipterocarp seeds and hunt wild game (primarily bearded pigs) that eat dipterocarp fruit (*8–10*). However, forest fragmentation and land cover change have transformed El Niño from a regenerative to a highly destructive phenomenon, one that triggers droughts and wildfires with increasing frequency and intensity, disrupts dipterocarp fruiting, interrupts wildlife reproductive cycles, and erodes the basis for rural livelihoods (*8*, *11*).

Protected areas [PAs, including IUCN (World Conservation Union) Categories I to VI] of sufficient extent and connectivity are required to sustain ecological integrity. Although 64% of Kalimantan's land area (>344,000 km^2) was allocated to industrial federal forest uses from 1967 to 1972, PAs were delineated or redrawn in 1984 and 1985 to maintain representative ecosystems and to be managed by the government (*12*). Since then, however, PAs have experienced concomitant threats from logging, wildfires, and conversion. Conserving Kalimantan's PAs requires current information on their condition and the nature of the threats they face.

Within PAs, we mapped lowland deforestation and measured deforestation rates within a nested design. We assessed Gunung Palung National Park (GPNP) in West Kalimantan and its 10-km buffer zone (2736 km^2 spatial extent) from 1988 to 2002, the West Kalimantan province (146,092 km^2) in 2001, and Kalimantan as a whole (537,040 km^2) in 2001 (Fig. 1) (*13*). We determined the distribution and condition of remaining lowlands [<500 m above sea level (a.s.l.) rather than <1000 m], because such forests contain distinctive dipterocarp habitats, the majority of vertebrates, the greatest canopy tree diversity, and the majority of land used by humans. Major drivers of deforestation were identified from West Kalimantan field studies (*13*) and contrasted with those reported for PAs elsewhere.

GPNP was selected for our detailed case study because of its biological importance (*12*) and our field-based research within GPNP and surrounds from 1985 to 2003. Because West Kalimantan contains the largest PA network of lowland dipterocarp forest in Kalimantan, this province served as our focal region. For the GPNP time-series and West Kalimantan analyses, we mapped forest and nonforest using 30-m spatial resolution satellite images. The Kalimantan-wide analysis used satellite images at a coarser spatial resolution (250 m). Images were classified into forest or nonforest classes with supervised classification and visual interpretation; results were validated with field and aerial surveys (from 1999 to 2003) and with reference satellite images with fine spatial resolution (1 m and 4 m) (*13*).

Our 14-year GPNP time-series analysis (Fig. 2) documents expansive and accelerating deforestation. Within the park's 10-km-

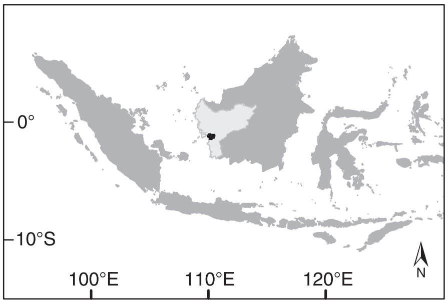

Fig. 1. Our case study area, GPNP and its surrounding 10-km buffer (black), is located on the southwest coast of the island of Borneo, in the province of West Kalimantan (light gray). Other areas of Borneo, surrounding Indonesian islands, and East Timor are depicted in dark gray.

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wide buffer strip surrounding the outer perimeter of the reserve, >70% of lowlands were deforested (46 km^2 year^{-1}) from 1988 to 2002, leaving <9% of the buffer in lowland forest. From 1988 to 2002, 38% of GPNP's lowlands were deforested (19 km^2 year^{-1}). Because of the high density and volume (50 to 120 m^3 ha^{-1}) of commercial timber (>90% of which is dipterocarps) in Kalimantan, intensively logged forests typically have ≥80% of the canopy basal area removed or destroyed (*8*). Deforestation within GPNP's buffer resulted primarily from intensive logging by timber concessions, followed by the clear cutting of residual stands by oil palm plantations [concessions and plantations comprise >70% of the buffer zone (Fig. 2D)]. After 1999, when <26% of the buffer remained forested, a rapid acceleration of deforestation (9.5% year^{-1}) occurred within GPNP (Fig. 3).

Lowland PAs such as GPNP are critical to maintaining Borneo's biodiversity. More than 420 resident bird and 222 mammal species occur on Borneo; 61% of these birds and 52 to 81% of the mammals are confined to lowland forests, including >50% of the endemic avian and >35% of the endemic mammalian species (*12*, *14*). GPNP harbors 178 or >70% of Bornean bird species (*15*) and >72 mammal species that depend on lowlands (*16*). Logging within GPNP's lowlands will adversely affect biodiversity; in addition to felling dipterocarp trees, logging removes the associated, asynchronously fruiting, hemiepiphytic figs (*Ficus* spp.) that serve as keystone resources for local vertebrates (*17*). In this region, at least 91 to 132 avian species (33 to 50% of the avifauna) respond negatively to lowland forest fragmentation and/or logging (*14*). Although mammalian response to such conditions varies by species and guilds, lowland-dependent species occur at much reduced densities in logged forests. For example, GPNP, with ~17% of Borneo's population of endangered orangutans, experienced a 21 to 33% reduction in orangutan densities in logged areas compared with unlogged areas (*18*).

Given the deforestation observed at our case study site, analyses were extended to evaluate all lowland PAs across West Kalimantan. In 1985, 76% (~29,000 km^2) of West Kalimantan PAs (38,500 km^2 spatial extent) contained well-drained lowland dipterocarp forest (fig. S2A). Nonlowland PAs were remote montane or swamp forests with relatively low economic value for timber. Our combined Geographic Information System and remote sensing analyses indicate that from 1985 to 2001, West Kalimantan's lowland PAs were reduced by 63% (~18,500 km^2), primarily by intensive logging. By 2001, only ~10,900 km^2 remained of protected lowland forest fragments larger than 10 km^2 (fig. S2B). Of the 64 remaining fragments, 36 were <50 km^2 (mean 20.0 km^2 ± 1.6 SE). Only 16 fragments (9385 km^2 total) are considered large enough (≥100 km^2) to support intact vertebrate fauna (*12*, *14*, *19*). The remote Betung Kerihun National Park (BKNP) (gazetted 1996) contains ~50% of the remaining protected lowlands in the province. Moreover, several potentially viable fragments are isolated (>50 km apart) (fig. S2B). Our Landsat Enhanced Thematic Mapper Plus (ETM+) analysis of 10-km buffers around West Kalimantan's World Conservation Monitoring Centre (WCMC) PAs (>100 km^2 total extent) reveals substantial deforestation; seven of eight buffers contained 0.5 to 31% lowland forest (mean 18.5% ± 5.3% SE). Although 45.6% of BKNP's buffer contains lowland forest, both this park and its buffer are currently being logged (*20*).

Across Kalimantan's other provinces (~387,000 km^2), we evaluated the condition of WCMC lowland PAs. Within ~23,100 km^2 of lowland PAs outside West Kalimantan (41% of the total protected area), only 33 fragments (≥100 km^2) remain forested (a loss of ~11,100 km^2, or 48% of the lowland forest cover) (fig. S3). Although 12 fragments contain sufficient area to support most vertebrates, 10 of these are isolates. Moreover, 69% of these "protected" forests (~8200 km^2) overlap industrial timber concessions or plantations (fig. S3).

Given this extensive reduction in Kalimantan's protected lowland forest, widespread effects are expected to cascade throughout their ecosystems. Because mast-fruiting dipterocarp communities satiate seed predators by employing a strategy of regional reproductive synchrony, the observed fragmentation is likely to trigger direct and indirect effects, including those demonstrated in frugivore-food web dynamics (*8*–*10*). Except for BKNP, large, intact protected lowlands no longer exist in Kalimantan (fig. S3). Therefore, threatened nomadic and large vertebrates with extensive lowland ranges are predicted to decline precipitously, especially carnivores, ungulates, and primates (e.g., the Malayan sun bear, *Helarctos malayanus*; the bearded pig, *Sus barbatus*; and the orangutan,

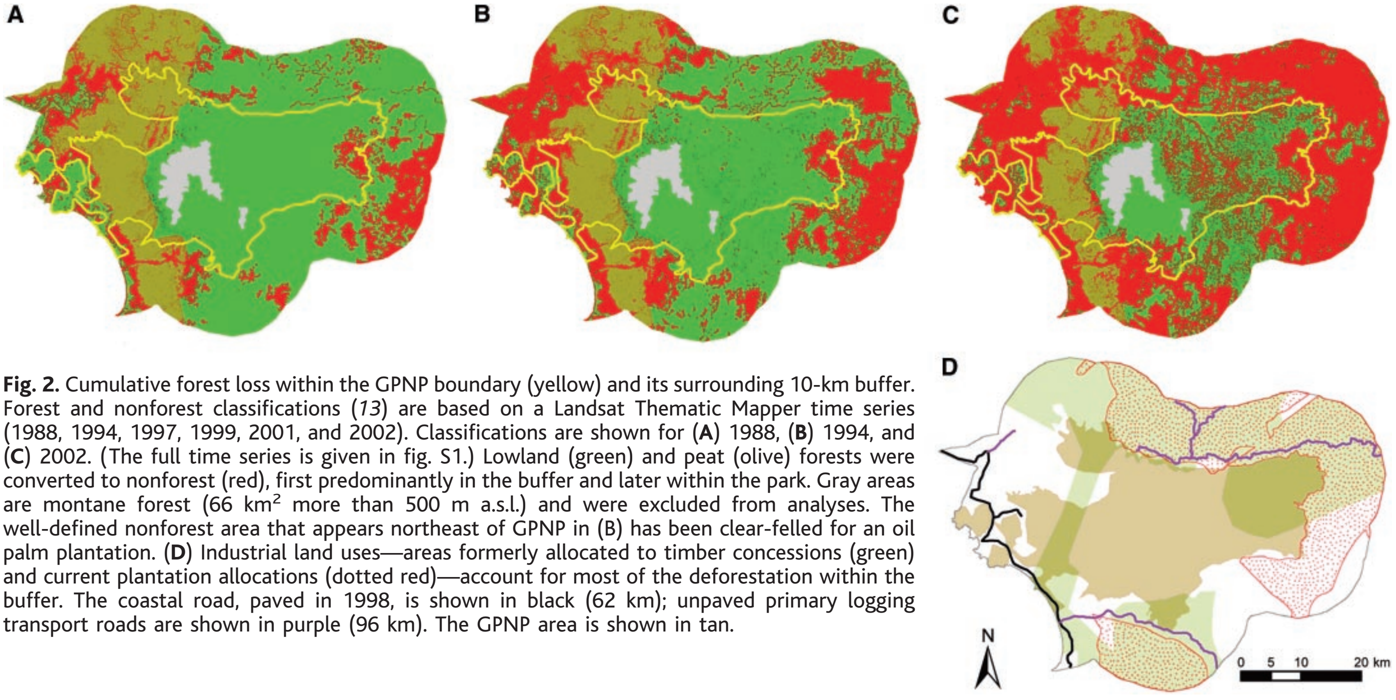

Fig. 2. Cumulative forest loss within the GPNP boundary (yellow) and its surrounding 10-km buffer. Forest and nonforest classifications (*13*) are based on a Landsat Thematic Mapper time series (1988, 1994, 1997, 1999, 2001, and 2002). Classifications are shown for (**A**) 1988, (**B**) 1994, and (**C**) 2002. (The full time series is given in fig. S1.) Lowland (green) and peat (olive) forests were converted to nonforest (red), first predominantly in the buffer and later within the park. Gray areas are montane forest (66 km^2 more than 500 m a.s.l.) and were excluded from analyses. The well-defined nonforest area that appears northeast of GPNP in (B) has been clear-felled for an oil palm plantation. (**D**) Industrial land uses—areas formerly allocated to timber concessions (green) and current plantation allocations (dotted red)—account for most of the deforestation within the buffer. The coastal road, paved in 1998, is shown in black (62 km); unpaved primary logging transport roads are shown in purple (96 km). The GPNP area is shown in tan.

Pongo pygmaeus). Preliminary evidence for such declines includes emaciated dead sun bears and bearded pigs radiotracked and observed in northeast Borneo and West and Central Kalimantan in 2000 and 2001 (*21*). Given local vertebrate extinctions after deforestation in Singapore (*22*), these Kalimantan results appear foreboding.

Kalimantan's PA forest loss provides a marked contrast to findings from Costa Rica (*23*), where negligible deforestation occurred within PAs from 1986 to 1997, and from the Brazilian Amazon, where PAs and especially extractive and indigenous reserves substantially inhibited forest cover loss (*24*, *25*). Moreover, interview-based assessments of 93 PAs worldwide (*26*) suggest that >83% of sites surveyed are maintaining or increasing their forest cover. Our contrasting figures of PA forest loss appear to be explained by distinctive drivers of deforestation occurring in Kalimantan.

Deforestation in Kalimantan's PAs is not primarily due to local human population density, smallholder agricultural clearing, or paved roads. Kalimantan has relatively low human population density and growth rates (1.9% annually for West Kalimantan between 1985 and 2000) with >40% of the total population in coastal cities (*12*, *13*). Moreover, inland rural populations live primarily in small villages (<5 adults per km^2) outside of PAs, where they historically engaged in smallholder agroforestry 0.01- to 0.015-km^2 parcels cleared per household, mostly from secondary forest, with 10- to 30-year agricultural fallows) and temporary off-farm labor (*27*). Neither can Kalimantan's deforestation be explained as a direct consequence of paved road construction or spontaneous interior migration as documented in the Amazon basin (*28*). In West Kalimantan in 2000, the extent of paved roads remained small (0.015 km/km^2) and primarily connected coastal ports; only 0.003 km/km^2 has been added since 1985.

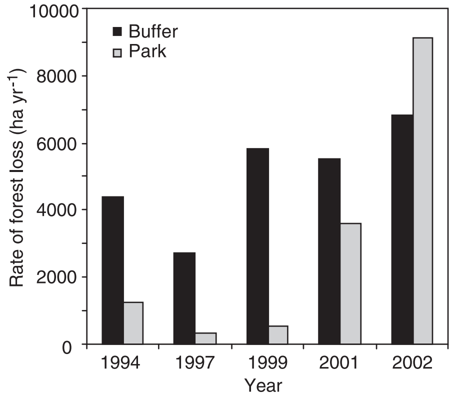

Fig. 3. Annual rates of forest cover change in the buffer zone and within GPNP from 1988 to 2002, from a 1988 baseline. During this period, a total of 628 km^2 of lowland dipterocarp forest within the park buffer and 257 km^2 within the park were lost, primarily through logging and conversion to plantations. After 1999, when ~75% of the buffer had been deforested, the rate of deforestation within the park increased to 9.5% year^{-1}.

Borneo is distinctive because of the dominance of the federal timber industry and the commercial value and stock of dipterocarp forests. Over the past two decades, the volume of dipterocarp timber exports (in cubic meters) from Borneo (Kalimantan, Sarawak, and Sabah) exceeded all tropical wood exports from tropical Africa and Latin America combined (*29*). Logging within PAs results from 20 to 30 years of forest overexploitation, evidenced by the recent and rapid decline in federal timber concessions (*4*, *5*). In West Kalimantan, only 6 of the original 72 concessions (formerly 79,000 km^2) allocated in the 1970s have an active harvest in 2003 and 2004. This represents a >94% reduction in logging operations' land area (now 4163 km^2). Within these active holdings, primary forest remains on ~15% (~600 km^2), distributed within a logged mosaic. Most concessions, having been depleted of their harvestable timber, are abandoned. In 2000, the Indonesian Ministry of Forestry reported that abandoned or expired timber concessions across Kalimantan contained <7 to 9% primary forest. Because timber was depleted within concessions, loggers illegally expanded their operations into PAs to maintain supplies for wood-based industries. More than 78% of the 18 concession operations we surveyed from 1999 to 2001 either directly harvested or received timber from PAs. At least 86 to 93% of these operations were processing this wood for international markets (*20*). Logging within PAs is further confirmed by our Landsat ETM+ analysis, which revealed concession-style logging active in all 10 WCMC PAs examined (>100 km^2) (table S1). Within these PAs, the length of industrial logging roads ranges from <1 km (BKNP) to 534 km (Bukit Raya) ($x = 175.4 \pm 53.0$ SE).

Logging within PAs is expected to increase for two main reasons. First, decentralization regulations implemented in 2001 now allow local districts to issue small logging parcel leases (1 km^2); this has resulted in the virtually uncontrolled harvest of remaining accessible lowland. For example, based on 6 months of field surveys in West Kalimantan's six timber producing districts, we determined that small parcels were granted locally to permit logging of >1750 km^2 of predominately protected lowlands or expired concessions during January to June 2001. Timber volume extracted from district-issued parcels increased by 650% from 2000. Second, widespread oil palm plantation establishment is converting logged lowland forest outside PAs, thus increasing pressure on PAs. From 1997 to 2002, the central government reclaimed several former West Kalimantan timber concessions (>20,000 km^2) and funded the clearance of residual wood, purportedly to establish oil palm plantations. Plantation establishment is promoted by state policies (e.g., interest-free loans from the national reforestation fund), often with encouragement (such as loans, loan guarantees, and export finance schemes) from international institutions. These incentives fueled a rapid expansion and conversion of lowlands to oil palm. In 2002, the area allotted to industrial plantations in West Kalimantan totaled ~35,000 km^2, with >31,000 km^2 slated for oil palm production, a 40-fold increase in the plantation area designated since 1992 (900 km^2). These areas are cleared of residual wood and burned to establish plantations.

Despite the declining resource base, Indonesia's wood-based industries have maintained excessive production capacity (*4*, *5*). For example, in West Kalimantan, 130 such industries had a total capacity of 5×10^6 m^3 year^{-1} in 2002 (*20*). Fourteen plywood industries alone (2.6×10^6 m^3 year^{-1}) exceeded provincial wood volume production capacity from federal timber concessions by 22% in 1994 and 1995, 132% in 1999 and 2000, and 162% in 2002 and 2003. Wood shortages are now met primarily through clearing for plantations and logging PAs. More than 52% of West Kalimantan's oil palm plantations were formerly timber concessions and clearing of their residual forest stands is either planned or completed (in the GPNP 10-km buffer, for instance). Most high-quality timber is now found in PAs; however, it is not protected in practice.

Rates and extent of lowland PA forest loss in Kalimantan far exceed previous projections (*30*). Stemming the flow of illegal wood from Borneo requires international efforts to document a legitimate chain-of-custody from the forest stand to consumers through independent monitoring. Indonesia's wood-based industries must demonstrate sufficient timber concession stock or reduce capacity. Timber and plantation operations must be closely monitored (with annual satellite-based assessments) with strictly enforced penalties to prevent further incursions into the PAs.

Failure to institute transparent and equitable land use solutions will lead to the irreversible ecological degradation of Borneo's terrestrial ecosystems. Effective frontier governance (*6*) and sound regional land-use planning are critical to protecting even uninhabited and remote PAs from regional, and increasingly international, market forces.

References and Notes

1. F. Achard *et al.*, *Science* **297**, 999 (2002).
2. D. C. Nepstad *et al.*, *Nature* **398**, 505 (1999).
3. C. Gascon, G. B. Williamson, G. A. B. da Fonseca, *Science* **288**, 1356 (2000).
4. C. Barr, in *Which Way Forward? People, Forests and Policymaking in Indonesia*, C. J. P. Colfer, I. A. P. Resosudarmo, Eds. (Resources for the Future, Washington, DC, 2002), pp. 191–220.

5. M. L. Ross, *Timber Booms and Institutional Breakdown in Southeast Asia* (Cambridge Univ. Press, Cambridge, 2000).
6. D. C. Nepstad *et al.*, *Science* **295**, 629 (2002).
7. J. Terborgh *et al.*, *Science* **294**, 1923 (2001).
8. L. M. Curran *et al.*, *Science* **286**, 2184 (1999).
9. L. M. Curran, M. Leighton, *Ecol. Monogr.* **70**, 101 (2000).
10. L. M. Curran, C. O. Webb, *Ecol. Monogr.* **70**, 129 (2000).
11. F. G. Siegert, G. Ruecker, A. Hinrichs, A. A. Hoffmann, *Nature* **414**, 437 (2001).
12. K. S. MacKinnon, G. Hatta, H. Halim, A. Mangalik, *The Ecology of Kalimantan* (Periplus Editions, Singapore, 1996).
13. Materials and methods are available as supporting material on *Science* Online.
14. F. R. Lambert, N. J. Collar, *Forktail* **18**, 127 (2002).
15. T. G. Laman, J. C. Gaither, D. E. Lukas, *Trop. Biodivers.* **3**, 281 (1996).
16. A. Blundell, *Trop. Biodivers.* **3**, 251 (1996).
17. M. Leighton, D. R. Leighton, in *Tropical Rain Forest: Ecology and Management*, S. L. Sutton, T. C. Whitmore, A. C. Chadwick, Eds. (Blackwell, Oxford, 1983), pp. 181–196.
18. A. E. Johnson, C. D. Knott, B. Pamungkas, A. J. Marshall, in preparation.
19. Laidlaw reports that $\geq$100 km^2 is required to maintain the majority of avian and mammalian species (*31*); $\geq$100 km^2 (and preferably $\geq$500 km^2) is required to maintain intact vertebrate faunas in the Sunda region (*12*, *14*).
20. T. Budiarto, *Investigasi Aktivitas Illegal Logging Di Propinsi Kalbar oleh Tim WWF-Indonesia, Kalimantan Barat 2003* (World Wide Fund for Nature, Pontianak, Indonesia, 2003).
21. S. T. Wong, thesis, University of Montana, Missoula (1997).
22. B. W. Brook, N. S. Sodhi, P. K. L. Ng, *Nature* **424**, 420 (2003).
23. G. A. Sanchez-Azofeifa, G. C. Daily, A. S. P. Pfaff, C. Busch, *Biol. Conserv.* **109**, 123 (2003).
24. S. Schwartzman, A. Moreira, D. C. Nepstad, *Conserv. Biol.* **14**, 1351 (2000)
25. D. C. Nepstad *et al.*, in preparation.
26. A. G. Bruner, R. E. Gullison, R. E. Rice, G. A. B. da Fonseca, *Science* **291**, 125 (2001).
27. D. M. Lawrence, M. Leighton, D. R. Peart, *Conserv. Biol.* **9**, 76 (1995).
28. D. C. Nepstad *et al.*, *For. Ecol. Manag.* **154**, 395 (2001).
29. International Tropical Timber Organization (ITTO), *Annual Review and Assessment of the World Tropical Timber Situation 1995* (Japan ITTO, Yokohama, 1996).
30. D. Holmes, *Deforestation in Indonesia: A Review of the Situation in Sumatra, Kalimantan, and Sulawesi* (World Bank, Jakarta, June 2002).
31. R. K. Laidlaw, *Conserv. Biol.* **14**, 1639 (2000).

32. We thank the Indonesian Institute of Sciences, Directorate General for Nature Conservation and Forest Protection, Ministry of Forestry, University of Tanjungpura, National (BAPPENAS) and Regional Development Planning Agency (BAPPEDA-KALBAR), timber and plantation company management, and the U.S. Agency for International Development (USAID)–Indonesia for sponsorship. The World Wide Fund for Nature-Indonesia-Kalbar-BKNP, Biodamar, YPPN, and Titian provided local nongovernmental support. A. Tjiu, Syrahirsyah, Darmawan, J. Belsky, S. Siebert, R. DeFries, D. McCauley, J. Fox, S. J. Lansing, M. Dove, C. O'Connor, D. Nepstad, W. Sandler, A. Doolittle, G. Paoli, J. Dempewolf, K. Wessels, J. Hewson, K. Pittman, A. Johnson, A. Gorog, E. DeMattia, K. Peay, F. Miller, J. Balch, D. Skelly, O. Schmitz, N. Sizer, A. Marshall, S. Unser, A. Purwono, J. Harting, T. Alexander, I. Zulkarnain, F. Soenoen, Ignatius, K. Atok, D. Rasel, Umar, and five anonymous reviewers provided invaluable contributions. Supported by the NASA Earth Sciences Program (grant nos. NAG 511335 and NAG 511161); a NASA Earth System Sciences Fellowship; NSF BE-CNH (grant no. 0215898); Space Imaging Inc.; the Yale School of Forestry and Environmental Studies; the Tropical Resources Institute; the Conservation Food and Health Foundation; the EPIQ-NRM2 Indonesia program; the East-West Center, Hawaii; and the University of Michigan.

Supporting Online Material

www.sciencemag.org/cgi/content/full/303/5660/1000/DC1
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Table S1

22 September 2003; accepted 6 January 2004

Photoreceptor Regulation of CONSTANS Protein in Photoperiodic Flowering

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Many plants flower in response to seasonal fluctuations in day length. The *CONSTANS* (*CO*) gene of *Arabidopsis* promotes flowering in long days. Flowering is induced when *CO* messenger RNA expression coincides with the exposure of plants to light. However, how this promotes CO activity is unknown. We show that light stabilizes nuclear CO protein in the evening, whereas in the morning or in darkness the protein is degraded by the proteasome. Photoreceptors regulate CO stability and act antagonistically to generate daily rhythms in CO abundance. This layer of regulation refines the circadian rhythm in *CO* messenger RNA and is central to the mechanism by which day length controls flowering.

Day length provides an environmental cue that allows plants to flower in response to the changing seasons (*1*). Long days (LDs) trigger flowering of *Arabidopsis*, and a genetic pathway controlling this response (*2*, *3*) is conserved in distantly related Angiosperms (*4*). In *Arabidopsis*, *CONSTANS* (*CO*) plays a central role in the induction of flowering by LDs and encodes a nuclear protein containing zinc fingers (*5*, *6*). *CO* mRNA abundance is regulated by the circadian clock and accumulates late in the day, when plants growing under LDs are exposed to light (*7*). Under these conditions, CO activates transcription of the *FT* gene, which encodes a RAF-kinase-inhibitor-like protein that promotes flowering (*7–11*). Activation of *FT* transcription is proposed to depend on posttranscriptional regulation of CO that is triggered by light, and therefore flowering under LDs occurs because of the coincidence of circadian-clock-controlled transcription of *CO* and light-mediated posttranscriptional regulation (*7*, *8*, *12*). How CO is regulated by light has not been described. We demonstrate that CO protein abundance and activity respond to light and define roles for photoreceptors in controlling these responses.

CO activity can be followed indirectly by measuring *FT* mRNA levels. The *35S::CO* plants, which overexpress *CO* mRNA at constant levels independently of the circadian clock or exposure to light, contain *FT* mRNA at higher abundance during the photoperiod than in the dark (*7*, *8*). A fusion of *FT* regulatory sequences to luciferase (LUC) was introduced into wild-type and *35S::CO* plants and accurately reported the up-regulation of *FT* caused by *CO* overexpression (fig. S1). The *35S::CO FT::LUC* plants were shifted from darkness to light of different wavelengths. Luminescence increased rapidly after exposure to white (W) or blue (B) light and more slowly when plants were exposed to far-red light (FR), but did not markedly increase in red light (R) (Fig. 1A). In *35S::CO* plants, *FT* mRNA abundance showed similar regulation to *FT::LUC*, whereas *CO* mRNA levels were not significantly altered by light (Fig. 1, B and C). Therefore, posttranscriptional regulation of CO activity by B and FR rapidly activates *FT* transcription after transfer from darkness, as described for the maintenance of CO activity after transfer from W (*8*).

We tested whether exposure to light regulates *FT* by influencing the abundance of CO protein. Fluorescence of GFP:CO (green fluorescent protein:CO) was detected in the nucleus of stomatal guard cells of *35S::GFP:CO* plants under W, B, or FR, but not in plants exposed to darkness or R (Fig. 2A). To follow native CO protein, antibodies

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