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Positive Feedbacks in the Fire Dynamic of Closed Canopy Tropical Forests

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The incidence and importance of fire in the Amazon have increased substantially during the past decade, but the effects of this disturbance force are still poorly understood. The forest fire dynamics in two regions of the eastern Amazon were studied. Accidental fires have affected nearly 50 percent of the remaining forests and have caused more deforestation than has intentional clearing in recent years. Forest fires create positive feedbacks in future fire susceptibility, fuel loading, and fire intensity. Unless current land use and fire use practices are changed, fire has the potential to transform large areas of tropical forest into scrub or savanna.

Fire is recognized as a historic but infrequent element of the Amazonian disturbance regime (*1*, *2*). Currently, however, fires in Amazonian forests are frequent because of the accidental spread from nearby pastures and the increased susceptibility of partially logged or damaged forests (*3*–*6*). Here, positive feedbacks associated with accidental forest fires are reported; these constitute a threat to the integrity of a large part of the Amazonian forest.

Field studies were concentrated in the Tailândia region (Fig. 1). Ten 0.5-ha plots (eight fire-affected and two control), spread over 100 km^2, were established in 1996 to study fire impacts on forest structure, biomass, and species composition (*3*). These plots were recensused after the dry season of 1997, during which eight of the plots burned to varying degrees. Fire recurrence, tree mortality, and biomass combustion levels within forests of different burn histories were quantified. In addition, combustible fuel mass was assessed with the planar intersect method (*7*) as adapted by Uhl and Kauffman (*8*, *9*).

We also examined characteristics of fires while they were occurring in four forest types (previously unburned, once-burned, twice-burned, and more than two previous burns) in December 1997. Direct observations of fires were made at widely scattered locations within a 150-km^2 area south of Tailândia. For each observed fire, flame heights and depths (the width of the flaming front) were measured or estimated (*10*). The time the fireline took to move across a known distance was used to calculate the rate of spread and was combined with flame depth data to calculate the average range of flame residence times at a point. Flame height was used as a conservative estimate of total flame length for the calculation of fireline intensity (*11*) because wind and slope were minimal (*12*).

The first fire to enter a forest usually moves slowly along the ground (Table 1) and is similar to a prescribed burn (<50 kW m^{-1}) in intensity (*13*). These fires consume little besides the dry leaf litter, but because of the characteristically thin tree bark [7.3 ± 3.7 mm for >20 cm diameter at breast height (dbh) (*8*)] protecting the cambium tissues, they still kill roughly 95% of the contacted stems >1 cm dbh. Large, thicker barked trees survive. After the fire, a rain of combustible fuels of all sizes falls from the standing dead trees (Table 1) (*14*). Fire damage and windthrow in these thinned forests continue to cause mortality for at least 2 years after the fire (*4*, *15*). Fuel levels rise substantially and the open canopy (50 to 70% cover) allows greater solar heating and air movement to dry out the forest fuels. Previously burned forests thus become susceptible to fire during common dry season weather conditions (*3*).

Previously burned forests were much more likely to burn than were unburned forests in 1997 (Table 1). Burned forests are often adjacent to fire-maintained pasture and agricultural plots and are therefore frequently exposed to sources of ignition. Second fires are faster moving and much more intense. We estimate heat release (*12*) of <7500 kW m^{-2} in first burns but of 75,000 kW m^{-2} or more in subsequent burns. Because of the increased flame depth, the residence time increases despite faster rates of spread, resulting in greater tree mortality. Large trees have little survival advantage during these more intense fires. Fire-induced tree mortality can be modeled as a function of bark thickness and fire residence time (*16*). For the observed fire characteristics and bark thickness distribution (*8*), no more than 45% of trees over 20 cm dbh are susceptible to fire-induced mortality in the initial fires. However, in recurrent fires, up to 98% of the trees become susceptible to fire-induced mortality.

The impacts of recurrent fires are much worse than those of initial fires. Higher mortality results in a very open canopy (10 to 40% cover), large inputs of combustible fuels, and faster drying. During the 1997 fires, substantial amounts of carbon were released to the atmosphere, with combustion reducing onsite biomass by approximately 15, 90, and 140 Mg ha^{-1} in first, second, and recurrent burns, respectively. Invading grasses and weedy vines add highly combustible live fuels to the already

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fuel-laden forest (*17*). Fires in highly degraded areas are significantly more severe in all respects (flame height, intensity, depth, residence time, and rate of spread). Recurrent fires have the potential to eradicate trees from the landscape (*18*).

Multitemporal analyses of satellite imagery [Landsat Thematic Mapper (TM)] were used to extend our study of fire in space and time in the Tailândia region and also in the Paragominas region (Fig. 1). Both regions have similar forests, pronounced dry seasons, and average annual rainfall of 1500 to 1800 mm (*19*). A linear mixture modeling methodology (*20*) was used to separate forest from nonforest and to classify burned forests in a series of images for 1280 km^2 near Paragominas (in 1984, 1991, 1993, and 1995) and for 2640 km^2 around Tailândia (in 1984, 1991, 1993, 1995, and 1997). The forest location and the area affected by fire were determined for the images of each region. Cross tabulation of the classified images provided a history of deforestation and forest burning throughout the study regions. The fire rotation, which is the amount of time required to burn an area equivalent to the entire forested area (*21*), was calculated for each region.

Areas that are minimally forested because of the recurrence of fire are likely to appear deforested in satellite imagery analyses [Landsat TM, Système Probatoire d'Observation de la Terre (SPOT), and Advanced Very High Resolution Radiometer (AVHRR)]. Visual inspection of paper Landsat TM images, as used to monitor deforestation in the Brazilian Amazon (*22*, *23*), is also expected to misclassify many burned forests as deforested areas. In this study, cross tabulation showed that, in comparison to unburned forest, once-burned forests were twice as likely to be classified as having been deforested, whereas twice- and thrice-burned forests were 11 and 15 times as likely to be classified as deforested.

We conducted a detailed study of deforestation in burned forests. Imagery of Paragominas for the period from 1993 to 1995 was used to test whether the deforestation of forests that had burned in 1992 was intentional (for example, slashed and burned for cattle pasture and crops) or accidentally induced by fire (that is, extremely thinned). Areas of forest that burned in 1992 that became either new slash or pasture were classified as intentional deforestation. These areas were generally adjacent to existing forest edges and had regular shapes. Forests that became "degraded pasture" (that is, second growth), an unlikely transition in just 2 years, were classified as accidental fire-induced deforestation. Fire-induced deforestation was generally irregular in shape and often occurred far from forest edges (Fig. 2).

In the Paragominas region, we estimate that accidental fire-induced deforestation increased deforestation estimates by 129% between 1993 and 1995. Correcting the deforestation estimate for this factor yields an intentional (that is, slash and burn) deforestation rate of 1.7% for the period from 1993

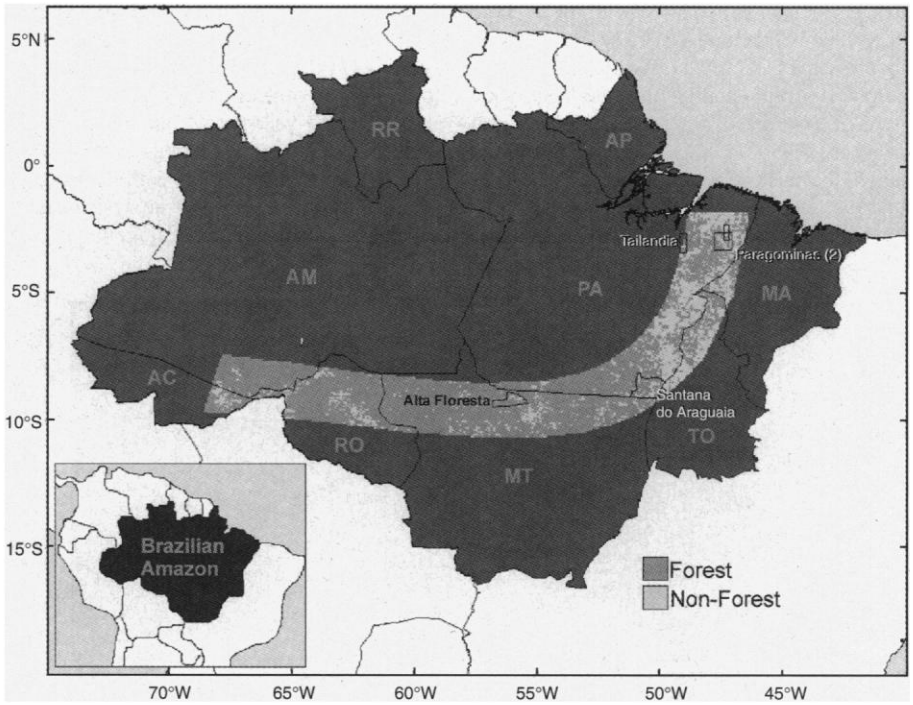

Fig. 1. Study regions within the Brazilian Amazon (dark shaded area; see inset at lower left). Fire incidence in Tailândia and Paragominas (rectangles) was investigated with multitemporal Landsat TM imagery. Landowner interviews in Pará (PA) and Mato Grosso (MT) were used to assess fire in additional study regions [Alta Floresta, Santana do Araguaia, and Paragominas (square)]. All study regions are located along the development frontier in a region known as the Arc of Deforestation (shown with lighter shading).

Table 1. Forest, fuel, and fire characteristics of four different forest types within the Tailândia study region.

Characteristics	Forest type			
	Unburned	First burn	Second burn	Third burn
Standing biomass (*3*)				
Live (Mg ha^{-1})	242	220	129	47
Dead (Mg ha^{-1})	53	50	71	116
Fuel load (*9*)				
1 hour (Mg ha^{-1})	1.3	3.3*	6.6****	
10 hours (Mg ha^{-1})	5.2	11.8*	16.9****	
100 hours (Mg ha^{-1})	16.8	36.8*	40.1***	
1000 hours (Mg ha^{-1})	15.5	124.9	106.1****	
Fuel height (cm)	15.8	47.8*	60.2****	
Fire characteristics (*10*)				
Flame heights (m)		0.13–0.46	0.32–0.88*	0.46****–1.33****
Flame depths (m)		0.08–0.20	0.18–0.49	0.29****–0.99****
Rate of spread (m min^{-1})		0.25	0.33	0.52****
Residence time (min)		0.32–0.80	0.49**–1.39*	0.66****–2.27****
Fireline intensity (kW m^{-1})†		4.4–55.0	82.5–412.2*	94.2****–728.3****
Height of crown scorch (m)‡		0.3–1.9	2.4–8.2**	4.6****–17.2****
Distribution of 1997 fire§				
Area burned (ha)	30964	33441	3196	30
Existing forest type that burned (%)	22.7	39.2	47.8	68.8

Asterisks indicate significant difference from unburned forest at $*P \leq 0.1$, $**P \leq 0.05$, $***P \leq 0.01$, and $****P \leq 0.001$ (Mann-Whitney test). †Fireline intensity calculated as $I = 258\ FL^{2.17}$, with flame height used to estimate flame length (FL) (*11*). ‡Height of crown scorch calculated as $h_s = 4.46\ I^{2/3} \times (60 - T)^{-1}$ (*T*, ambient temperature) (*28*). §Only covers fires in Tailândia occurring before the October TM image. Additional fires burned large areas of both previously unburned and burned forests within the study region between 4 and 10 December 1997. The percentage burned signifies the amount of the remaining unburned and previously once-burned, twice-burned, and thrice-burned forests that burned (for example, 39.2% of all forests that were already once-burned burned again in 1997).

to 1995, which is in accord with the average (1.8%) deforestation rate before the El Niño–induced fires of 1992/1993 (Table 2). This surprising result implies that the basin-wide jump in estimated deforestation rates from 1993 to 1995 (*23*, *24*) may have occurred largely because of the widespread forest fires of 1992 and 1993.

There have been no known analyses of the natural fire rotation in lowland tropical rainforests, but the limited data from charcoal studies (*1*) imply a fire rotation of hundreds or thousands of years. Fire-return intervals of less than 90 years can eliminate rainforest tree species, whereas intervals of less than 20 years may eradicate trees entirely (*25*). On the basis of our time series analysis of imagery, we calculate that Paragominas' and Tailândia's forests are currently experiencing fire rotations of between 7 and 14 years. Previously burned forests are even more prone to burning, with calculated fire rotations of less than 5 years.

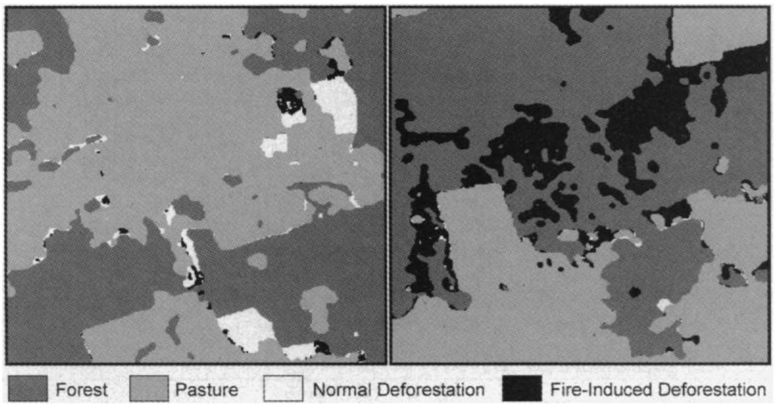

Fig. 2. Two 64-km^2 imagery subsections illustrating the differences in location and form of normal deforestation (for example, caused by slash and burn for pasture and crops) and fire-induced deforestation, caused by accidental forest fires.

Table 2. Deforestation and forest burning in several study regions determined with two different methodologies: Imagery analyses were based on multitemporal analyses of Landsat TM imagery; interview-based data were from a 1996 landowner interview study of fire and deforestation. Comparison of these data with satellite imagery has shown them to be very conservative with regard to fire and deforestation (*6*, *29*). An additional 85 interviews were conducted in Rondonia and Acre. Rondonia experienced fire but was excluded because of the small amount of total forested area (72 km^2). Acre had no recorded occurrence of accidental forest fire and is apparently wetter and less seasonal.

	Imagery analyses		Interview-based data		
Study region	Tailândia	Paragominas	Paragominas*	Santana do Araguaia	Alta Floresta
Area (km^2)	2640	1281	1572	4718	1000
Total deforested†					
1984	9.8%	38.1%			
1991	27.4%	48.7%			
1993	32.9%	55.0%	43.5%	35.6%	31.3%
1994			44.6%	36.1%	32.9%
1995	40.9%	64.0%	45.9%	36.7%	33.7%
1997	44.3%				
Average annual rate	1.8%	2.3%			
Annual % of forest burning‡					
1984		9.6%			
1991	1.0%	4.7%			
1993	23.1%	45.9%			
1994			0.4%	5.6%	1.5%
1995	2.9%	1.3%	1.2%	3.0%	3.7%
1997	31.2%				
Fire rotation§					
Years	7–14	7–13	125 (35)‖	23	38

*Additional area of Paragominas County, which has 51% overlap with the imagery study region. †Numbers give the percentage of the study region that was deforested for the given year. For the imagery-analyzed areas, the long-term deforestation rate is the average annual percentage cleared since incorporation (Tailândia in 1978 and Paragominas in 1960). ‡Numbers show the percentage of the standing forest that burned in a given year. Cochrane and Souza's (*20*) technique detects fires more than 1 but less than 2 years old. 1983, 1992, and 1997 were El Niño years, and the resultant fires were detected in the 1984, 1993, and 1997 images. §Time necessary to burn an area equal to the total forested area, based on the average annual percentage of forest burning, with the understanding that some areas will burn several times whereas others may not burn at all during the interval. Tailândia and Paragominas are presented as ranges, because the methodology used detects fires 1 to 2 years old. ‖Interview data were systematically underestimated (*29*); the number in parentheses shows the fire rotation if this underestimate is corrected.

Results derived from satellite images were compared to data from three other regions (7290 km^2) of the Amazon. A total of 117 randomly chosen landowners from Pará and Mato Grosso were asked to mark deforested and burned forest areas on Landsat TM image prints (Fig. 1 and Table 2). Calculated fire rotations for each region were similar to one another (Table 2), indicating that the entire region between Mato Grosso and northeastern Pará may be experiencing the same fire regime. Though rotation times were longer than those determined by analysis of TM images, the landowner estimates of forest area burned were for non–El Niño years (1994 and 1995). The resultant fire rotation calculations are therefore very conservative, because this study's multitemporal analyses show that 90% of forest burning has occurred during El Niño years.

The average rate and intensity of forest burning and deforestation can be expected to increase as previously burned forest area expands. A positive feedback exists between forest fires, future fire susceptibility, fuel loading, and fire severity. In the past several years, roughly 50% of the remaining forests in the study regions around Paragominas and Tailândia have burned, 20% having burned more than once. First-time burns can be controlled and put out manually with minimal equipment, but more than 30% of the observed fires in previously burned forest had fireline intensities that were beyond the limits of manual control (*13*). Left unchecked, the current fire regime will result in an inexorable transition of the entire area to either scrub or grassland (*25*). Effects on the regional climate, biodiversity, and economy are likely to be extreme. These fire-induced changes will take several years to occur but are likely to be irreversible (*26*, *27*) under current climatic conditions.

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9. Fuel load quantities, divided into standard time-lag size classes (1 hour, 10 hour, 100 hour, and 1000 hour; corresponding to 0 to 0.6, >0.6 to 2.5, >2.5 to 7.6, and >7.6 cm in diameter), fuel height, and leaf litter depth were measured along randomly directed 10-m transects at three points within each plot (125, 250, and 375 m). Additional fuel load measurements were made in the vicinity of all observed fires.
10. At each observation site (n = 44), roughly 10 m of fireline was observed every 30 s for several minutes (average observation time, 7.4 min), and the average minimum and maximum of each flame characteristic were recorded. Flareups of short duration or small area were noted separately.
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14. Leaf fall from damaged trees begins within 2 days of a burn. We have observed contiguous layers of leaf litter in recently burned forests in close proximity to smoldering logs. Frequent observations by local residents that forest stands often burn more than once in a season may be explained by smoldering logs reigniting fires once litter depths become sufficient to carry fire through the stand.
15. The mortality of trees (>10 cm dbh) in previously unburned forests that burned in 1995 was 38% 1 year after the fire and 68% at the end of the second year. Annual mortality in unburned forest during this time period was <1%.
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29. In Paragominas, burns detected in the imagery were compared with data from landowner questionnaires (n = 75) that described fire history from 1982 to 1995. Questionnaire data included 51.4% of the study region and showed 100% detection of reported fires that occurred within 1 year of the image date. Comparisons between the area reported burned by landowners with data from the imagery classifications showed that the area burned was systematically underreported ($P < 0.001$; sign test) by an average of 43%. Only small fires (<50 ha) were overestimated by landowners.
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The Nature of the Principal Type 1 Interferon–Producing Cells in Human Blood

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Interferons (IFNs) are the most important cytokines in antiviral immune responses. "Natural IFN-producing cells" (IPCs) in human blood express CD4 and major histocompatibility complex class II proteins, but have not been isolated and further characterized because of their rarity, rapid apoptosis, and lack of lineage markers. Purified IPCs are here shown to be the $CD4^+CD11c^-$ type 2 dendritic cell precursors (pDC2s), which produce 200 to 1000 times more IFN than other blood cells after microbial challenge. pDC2s are thus an effector cell type of the immune system, critical for antiviral and antitumor immune responses.

Interferons were discovered in the 1950s as factors rapidly produced by virus-infected cells that enable neighboring cells to resist virus infection (*1*). IFN-α (leukocyte IFN) and IFN-β (fibroblast IFN), the two type 1 antiviral IFNs, are distinct from type 2 IFN-γ produced by effector T cells. Specialized leukocytes, the "natural IFN-producing cells" (IPCs), were shown to be the chief IFN-α producers in response to enveloped viruses, bacteria, and tumor cells (*2–14*). IPCs express CD4 and major histocompatibility complex (MHC) class II, but lack hematopoietic-lineage markers (*2–14*). The nature of IPCs—whether they represent dendritic cells (*6*, *12*, *14*) or cells of a distinct lineage (*7*, *9*)—has been controversial. There is a progressive loss of $CD4^+$ T lymphocytes and functional IPCs during human immunodeficiency virus (HIV) infection (*15*, *16*). Preservation of IPCs is associated with protection from opportunistic infections, suggesting the importance of IPCs in the host defense (*16*).

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A plasmacytoid cell type from human tonsils and blood that lacks lineage markers also expresses CD4 and MHC class II (*17–21*). These cells differentiate into type 2 dendritic cells (DC2s) when cultured with interleukin-3 (IL-3) and CD40 ligand (*19*, *21*). Unlike monocyte-derived type 1 dendritic cells (DC1s) that induced type 1 T helper cell (T_H1) differentiation, DC2s induced type 2 T helper cell (T_H2) differentiation (*21*). Here we investigated whether DC2 precursors (pDC2s) represent IPCs. Human peripheral blood cells were separated into the following populations (*19*, *21*): (i) monocytes (over 90% purity), obtained by centrifugation through 52% Percoll, then magnetic bead depletion of B, T, and natural killer (NK) cells; (ii) $CD4^+CD3^-CD11c^+$ immature DCs (99% purity) and (iii) $CD4^+CD3^-CD11c^-$ pDC2s (99% purity), obtained by magnetic bead depletion of B, T, NK cells, and monocytes, followed by fluorescence-activated cell sorting (FACS) (Fig. 1, A and B); (iv) pDC2-depleted blood mono-

Table 1. Precursor DC2 cells are the natural IFN-producing cells. Cells (2 × 10^5) were cultured for 24 hours with HSV. Without HSV, IFN activity from different cell types was less than 12.5 U/ml (*23*). PBMC: total blood mononuclear cells; pDC2-dep: blood mononuclear cells positively selected for expressing CD3, CD11c, CD19, CD14, and CD56; pDC2-enrich: blood mononuclear cells that were depleted of cells expressing CD3, CD19, CD14, and CD56; pDC2: FACS-sorted $CD4^+CD11c^-lin^-$ cells; $CD11c^+$ DC: FACS-sorted $CD11c^+lin^-$ immature DCs; Mo: monocytes; DC1: monocyte-derived DCs after 6 days of culture with either granulocyte-macrophage colony-stimulating factor (GM-CSF) + IL-4 or GM-CSF + IL-4 + CD40 ligand (*21*); DC2: pDC2-derived DCs after 6 days of culture with IL-3 or IL-3 + CD40 ligand (*23*). ND, not determined.

	IFN (U/ml)							
	PBMC	pDC2-dep	pDC2-enrich	pDC2	$CD11c^+$DC	Mo	DC1	DC2
Exp. 1	500	ND	2,800	89,800	120	ND	<12.5	1,100
Exp. 2	40	<12.5	180	20,000	<12.5	350	<12.5	<12.5
Exp. 3	700	40	2,800	638,000	70	90	ND	ND