

Forest–climate interactions in fragmented tropical landscapes

William F. Laurance

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá, and Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), C.P. 478, Manaus, AM 69011-970, Brazil
(laurancew@tivoli.si.edu)

In the tropics, habitat fragmentation alters forest–climate interactions in diverse ways. On a local scale (less than 1 km), elevated desiccation and wind disturbance near fragment margins lead to sharply increased tree mortality, thus altering canopy-gap dynamics, plant community composition, biomass dynamics and carbon storage. Fragmented forests are also highly vulnerable to edge-related fires, especially in regions with periodic droughts or strong dry seasons. At landscape to regional scales (10–1000 km), habitat fragmentation may have complex effects on forest–climate interactions, with important consequences for atmospheric circulation, water cycling and precipitation. Positive feedbacks among deforestation, regional climate change and fire could pose a serious threat for some tropical forests, but the details of such interactions are poorly understood.

Keywords: atmospheric circulation; carbon dynamics; edge effects; fire; forest hydrology; microclimate

1. INTRODUCTION

The fragmented landscape is becoming one of the most widespread features of the modern world. Nowhere is habitat fragmentation occurring more rapidly than in the tropics, where several hundred million hectares of forest have been destroyed during the past few decades (Lanly 1982; Achard *et al.* 2002). The correlated processes of habitat loss and fragmentation are probably the greatest single threat to tropical biodiversity (Laurance & Bierregaard 1997) and alter many ecosystem functions such as carbon storage, biogeochemical cycling and regional hydrology (Lean & Warrilow 1989; Kauffman *et al.* 1995; Fearnside 2000).

I therefore synthesize the available information on the impacts of habitat fragmentation on forest–climate interactions in the tropics. Although much is uncertain, it is apparent that fragmentation alters such interactions in diverse ways and at varying spatial scales. Understanding these interactions and their effects on forest functioning is essential both for interpreting the effects of global climate change on tropical ecosystems and for assessing the impacts of rapid forest conversion on the physical and biological environment.

2. SIZE AND SHAPE OF FRAGMENTS

Obviously, the processes of deforestation and forest fragmentation are inextricably linked. As land conversion proceeds, remnant forest patches usually persist (either by chance or design) within a matrix of drastically modified land, such as cattle pastures, slash-and-burn farming plots

or scrubby regrowth. Most human-dominated landscapes are numerically dominated by small (less than 100 ha) forest fragments (figure 1), although a sizeable percentage of the remaining forest may persist in a few large (greater than 1000 ha) fragments (Ranta *et al.* 1998; Gascon *et al.* 2000; Cochrane & Laurance 2002).

One of the most critical consequences of habitat fragmentation is a drastic increase in the amount of abrupt, artificial forest edge. Prevailing land uses, such as slash-and-burn farming and cattle ranching, typically create irregularly shaped fragments with large amounts of edge (figure 2). In the Brazilian Amazon, for example, the area of forest in 1988 that was fragmented (less than 100 km² in area) or vulnerable to edge effects (less than 1 km from the forest edge) was over 150% larger than that which had actually been deforested (Skole & Tucker 1993). Remote-sensing analyses suggest that because of rapid deforestation, almost 20 000 km of new forest edge is being created each year in Brazilian Amazonia alone (W. Chomentowski, D. Skole and M. A. Cochrane, personal communication).

3. MICROCLIMATE AND WIND

On a local scale (less than 1 km), deforestation reduces plant evapotranspiration, humidity, effective soil depth, water-table height and surface roughness, and increases soil erosion, soil temperatures and surface albedo (Wright *et al.* 1996; Gash & Nobre 1997). Thus, the cleared lands that surround forest fragments differ greatly from forest in their physical and hydrological characteristics.

The forest edge is the interface between fragments and their adjoining clearings, and the proliferation of edge has major impacts on many ecological processes. Undisturbed rainforests are dark and humid, with stable temperatures, little wind and almost continuous canopy cover (Lovejoy

One contribution of 17 to a Theme Issue 'Tropical forests and global atmospheric change'.

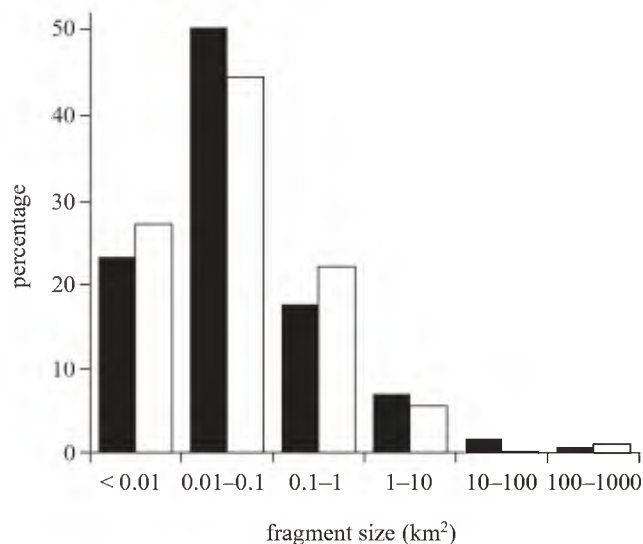


Figure 1. In human-dominated landscapes, most forest fragments are small (less than 1 km²). Data shown are for two fragmented areas in eastern Amazonia (Paragominas, filled bars; Tailândia, open bars) (after Cochrane & Laurance 2002).

et al. 1986; Laurance *et al.* 2002a), but when joined by clearings these conditions are sharply altered. On newly created edges, elevated temperatures, reduced humidity and increased sunlight and vapour pressure deficits can penetrate at least 40–60 m into fragment interiors (Kapos 1989; Didham & Lawton 1999; Sizer & Tanner 1999). Such changes increase evapotranspiration in understory vegetation, leading to depleted soil moisture and creating stresses for drought-sensitive plants (Kapos 1989; Malcolm 1998).

In addition, the edges of habitat remnants are exposed to increase wind speed, turbulence and vorticity (Bergen 1985; Miller *et al.* 1991). Wind disturbance is an important ecological force in the tropics, especially in the cyclonic and hurricane zones from *ca.* 7–20° latitude (Webb 1958; Whitmore 1975; Lugo *et al.* 1983), but also in equatorial forests affected by convective storms (Nelson *et al.* 1994) and prevailing winds (Laurance 1997). Winds striking an abrupt forest edge can exert strong lateral-shear forces on exposed trees and create considerable downwind turbulence for at least 2–10 times the height of the forest edge (Somerville 1980; Savill 1983; Reville *et al.* 1990). Greater wind speeds increase the persistence and frequency of wind eddies near edges that can heavily buffet the upper 40% of the forest (Bull & Reynolds 1968).

These physical alterations lead to sharply increased tree mortality and damage within 100–300 m of fragment margins (figure 3; Ferreira & Laurance 1997; Laurance *et al.* 1998a). In central Amazonia, large (greater than 60 cm diameter) trees are especially vulnerable, dying nearly three times faster near edges than in forest interiors (Laurance *et al.* 2000). Some trees near edges simply drop their leaves and die standing (Lovejoy *et al.* 1986; Sizer & Tanner 1999), apparently because sudden changes in moisture, temperature or light exceed their physiological tolerances. Many others are killed by winds, as evidenced by the fact that trees near edges are significantly more likely to be snapped or uprooted than those in forest interiors (D'Angelo *et al.* 2002).

Chronically elevated tree mortality has myriad effects. It fundamentally alters canopy-gap dynamics (Ferreira & Laurance 1997; Laurance *et al.* 1998a; Lewis 1998), which influences forest structure, composition and diversity. Smaller fragments often become hyper-disturbed, leading to progressive changes in floristic composition (Laurance 1997). New trees regenerating near forest edges are significantly biased toward disturbance-loving pioneer and secondary species and against old-growth, forest-interior species (Viana *et al.* 1997; Laurance *et al.* 1998b). Lianas—important structural parasites that reduce tree growth, survival and reproduction—increase in density near edges and may further elevate tree mortality (Oliveira-Filho *et al.* 1997; Viana *et al.* 1997; Laurance *et al.* 2001). Leaf litter accumulates near edges (Carvalho & Vasconcelos 1999; Sizer *et al.* 2000) as drought-stressed trees shed leaves, and may negatively affect seed germination (Bruna 1999) and seedling survival (Scariot 2001). Finally, fragmented forests exhibit a marked decline of biomass (Laurance *et al.* 1997), increased necromass and accelerated carbon cycling (Nascimento & Laurance 2004), and are probably a non-trivial source of atmospheric carbon emissions (Laurance *et al.* 1998c; Nascimento & Laurance 2004).

Accelerated tree mortality directly affects forest–climate interactions by increasing the density of tree-fall gaps and altering the canopy structure. Recurring canopy damage exacerbates edge-related changes in microclimate, increasing daytime temperature (Malcolm 1998) and vapour pressure deficits (Camargo & Kapos 1995) and altering the amount and spectral quality of light reaching the forest floor (Turton 1992). Such changes create physiological stresses for sensitive plant species (Kapos *et al.* 1993; Bruna 2002). Gaps in the canopy are also prone to wind vortices that can kill or damage adjoining trees (Bull & Reynolds 1968; Reville *et al.* 1990) and can become foci for recurring canopy disturbances (Laurance 1997). Thus, edge-related changes in microclimate can be substantially magnified by elevated canopy damage near edges.

4. EDGE AND LANDSCAPE STRUCTURE

The physical structure of edges strongly influences forest–climate interactions. In the tropics, newly formed edges (less than 5 years old) are structurally open and thus more permeable to lateral light and hot dry winds than are older edges, which tend to become 'sealed' by a proliferation of vines and second growth (Kapos *et al.* 1993; Camargo & Kapos 1995; Didham & Lawton 1999). Wind damage, however, is unlikely to lessen as fragment edges become older and less permeable, as downwind turbulence increases when edge permeability is reduced (Savill 1983). Nevertheless, edge structure influences the intensity of many edge effects, and land-use practices that repeatedly disturb fragment margins (such as regular burning) can have severe impacts if they prevent natural edge closure (Cochrane *et al.* 1999; Didham & Lawton 1999; Gascon *et al.* 2000).

In addition, edge orientation (aspect) can affect microclimatic parameters that influence plant germination, growth and survival (Turton & Freiburger 1997). For example, heat and desiccation stress are highest on edges facing the afternoon sun (Malcolm 1998), whereas

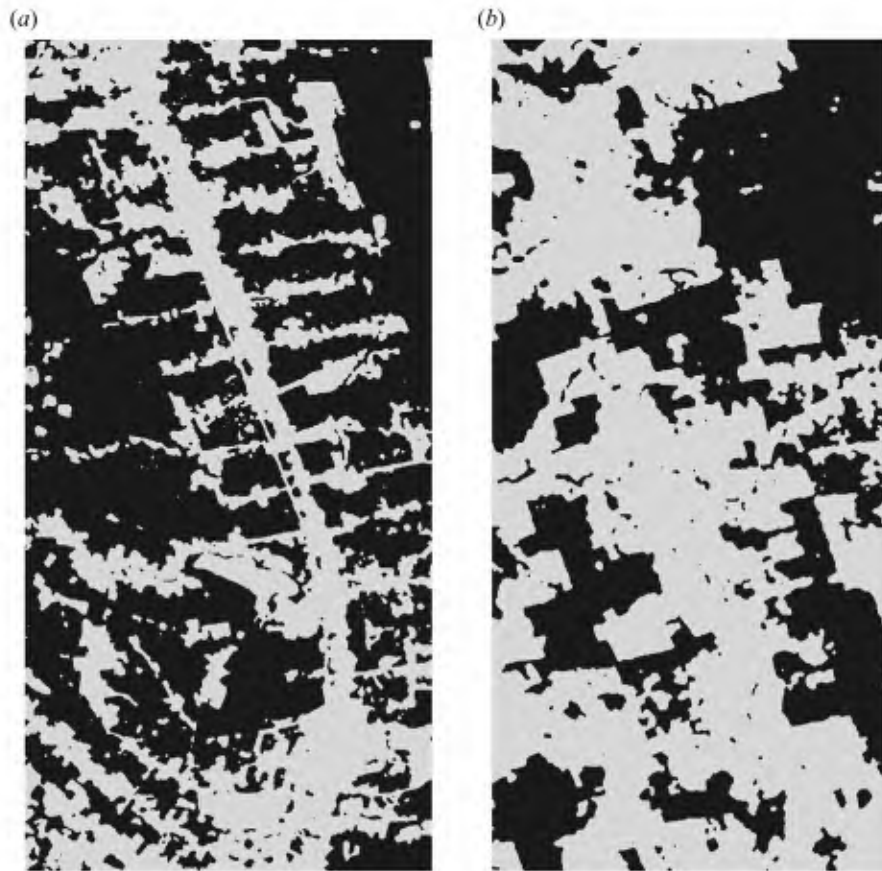


Figure 2. Habitat fragmentation leads to a proliferation of forest edge, as shown in two landscapes in eastern Amazonia (each 600 km² in area; dark areas are forest and light areas are mostly pastures). (a) Tailândia, a government-sponsored colonization project, shows the characteristic ‘fishbone’ pattern of deforestation, whereas (b) Paragominas is a cattle-ranching and logging frontier. For each square kilometre of cleared land in these two areas, an average of 1.5 km of forest edge was created (after Cochrane & Laurance 2002).

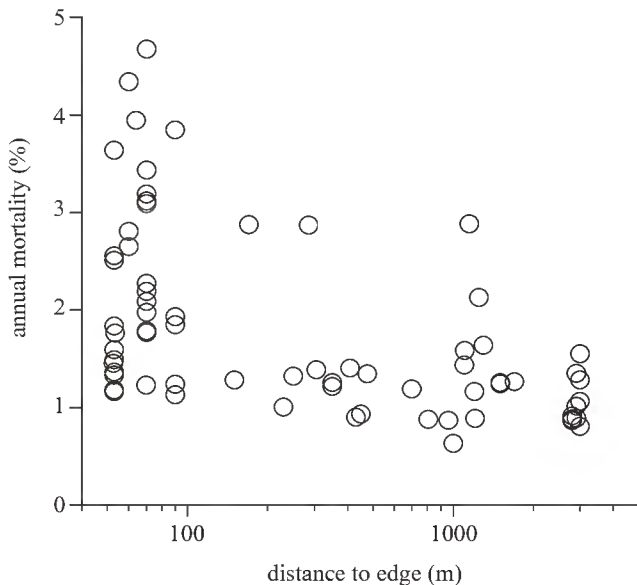


Figure 3. In rainforests, tree mortality rises sharply near forest edges. Data shown are from a long-term experimental study of forest fragmentation in the central Amazon (after Laurance *et al.* 1998a).

wind disturbance (Kapos *et al.* 1993; Laurance 1997) and atmospheric deposition of pollutants (Weathers *et al.* 2001) are greatest on edges exposed to prevailing winds.

Fragment size and isolation also influence forest–climate interactions. Large clearings surrounding fragments have greater ‘fetch’ than small clearings, resulting in higher wind velocities and increased structural damage to adjoining forest stands (Somerville 1980; Savill 1983). Desiccation and temperature extremes are also likely to increase with clearing size. Fragments that are small or have irregular boundaries are especially vulnerable to edge effects, because any point within the fragment will be influenced by multiple nearby edges, rather than a single edge (Malcolm 1994, 1998). Empirical and modelling studies in central Amazonia suggest that the impacts of edge-related tree mortality will rise sharply once fragments fall below 100–400 ha in area, depending on fragment shape (Laurance *et al.* 1998a).

Finally, the structure of modified vegetation surrounding fragments can clearly affect forest–climate interactions. Fragments surrounded by regrowth forest are somewhat buffered from damaging winds and harsh external microclimates, and suffer lower edge-related tree mortality than do those encircled by cattle pastures (Mesquita *et al.* 1999). The hydrology of different vegetation types also varies considerably. For example, in the eastern Amazon, degraded cattle pastures (which are dominated by shrubs and small trees) contain deep-rooted plants that absorb deep soil water and thereby maintain moderately high rates of evapotranspiration during the dry season. This is in sharp contrast to managed pastures (grass

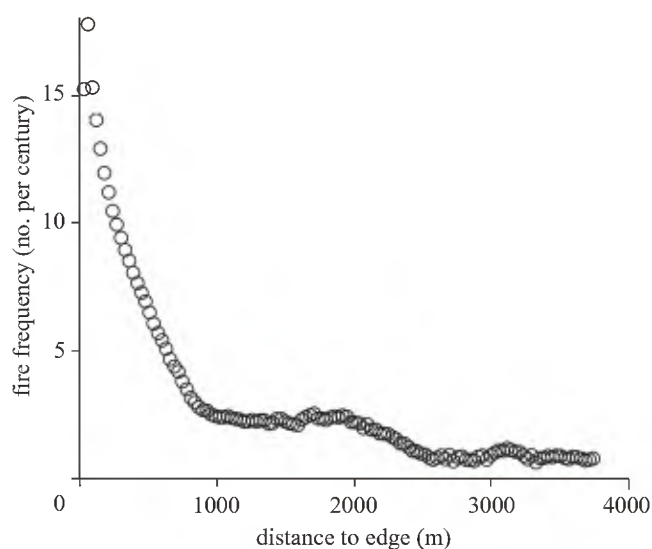


Figure 4. Estimated fire frequencies as a function of distance from forest edge for the Tailândia region in eastern Amazonia. Data are based on remote-sensing imagery spanning a 14-year period (after Cochrane & Laurance 2002).

monocultures), which contain virtually no deep roots and exhibit little evapotranspiration during dry periods (Nepstad *et al.* 1994). Hence, fragments surrounded by managed pastures may experience greater desiccation stress than those surrounded by degraded pastures or regrowth, because the former fail to recycle water vapour into the atmosphere during the critical dry-season months.

5. EDGE-RELATED FIRES

Except when subjected to strong droughts (e.g. Leighton & Wirawan 1986; Peres 1999; Gudhardja *et al.* 2000; Barlow & Peres 2004), large unbroken tracts of humid tropical forest are usually highly resistant to fire, both because the dense canopy maintains humid, nearly windless conditions and because fine fuels such as leaf litter, which can be highly flammable, decompose rapidly (Nepstad *et al.* 1999). When fragmented, however, tropical forests become drastically more vulnerable. Fragments tend to have dry fire-prone edges with large amounts of litter and wood debris (Cochrane *et al.* 1999; Nascimento & Laurance 2004). They are also frequently juxtaposed with cattle pastures, which are regularly burned to control weeds and promote new grass. In addition, fragments are particularly vulnerable to periodic droughts, which increase already-high tree mortality and litter production (Laurance & Williamson 2001) and thereby augment forest fuels at a time when conditions are driest. Finally, forest fragments are frequently disturbed by logging (Laurance & Cochrane 2001), which further exacerbates forest desiccation, fuel loading and vulnerability to fire (Uhl & Kauffman 1990; Holdsworth & Uhl 1997; Siegert *et al.* 2001).

In the eastern Amazon, surface fires that originate in adjoining pastures can penetrate large distances into fragment interiors (figure 4; Cochrane & Laurance 2002). Although confined to the forest floor, such fires are highly destructive because rainforest plants are poorly adapted for fire, having thin bark and no underground buds from which to resprout (Uhl & Kauffman 1990). Even light

fires kill up to half of all trees and virtually all vines (Cochrane & Schulze 1999; Barlow *et al.* 2003; Barlow & Peres 2004). Subsequent fires are far more intense because dying plants increase fuel loads and reduce canopy cover, promoting forest desiccation (Cochrane *et al.* 1999). Forest fragments affected by such recurring fires may 'implode' over time as their margins collapse inward (Gascon *et al.* 2000). Because surface fires can penetrate up to several kilometres into forest interiors, even very large (greater than 100 000 ha) forest fragments may be vulnerable (Cochrane & Laurance 2002).

Spatial and temporal variability in rainfall have major effects on fire frequency and intensity. Fires are especially problematic in tropical regions affected by strong dry seasons or by periodic droughts—such as occur during El Niño events throughout large areas of the neotropics, Southeast Asia and Australasia (Leighton & Wirawan 1986; Kinnaird & O'Brien 1998; Curran *et al.* 1999; Cochrane *et al.* 1999; Nepstad *et al.* 1999; Barlow & Peres 2004). In the Brazilian Amazon, more than one-third of the closed-canopy forest experiences soil-water deficits during strong droughts (Nepstad *et al.* 2001) and some 45 million hectares (13% of the total forest area) may already be vulnerable to edge-related fires (Cochrane 2001).

6. REGIONAL EFFECTS

Insights into land–atmosphere interactions at landscape to regional scales (*ca.* 10–1000 km) derive from simulation models that may integrate data from weather satellites, doppler radar, radiosonde sites, micrometeorological studies and other observations. Conclusions of larger-scale models (including global-circulation and mesoscale models) are more tenuous than those focusing on local processes, given the potentially great complexity of interacting factors at widely varying spatial scales. Rather than attempt a detailed review, I focus on a few key findings.

A number of regional modelling studies have attempted to project the future climatic impacts of severe tropical deforestation. To simplify the models, several studies have assumed complete conversion of Amazonian (e.g. Nobre *et al.* 1991; Dickinson & Kennedy 1992; Gash & Nobre 1997; Lean & Rowntree 1993) or Southeast Asian (Henderson-Sellers *et al.* 1993) forests to pasture or savannah. Although results have varied, most studies predict that uniform deforestation will lead to markedly decreased regional rainfall (*ca.* 20–30%) as well as lower evaporation, cloud cover and soil moisture, and higher albedo and surface temperatures (e.g. Lean & Rowntree 1993; Gash & Nobre 1997; Sud *et al.* 1996).

However, regional patterns of forest loss are never uniform. For example, tropical deforestation is much greater in southeastern Amazonia than elsewhere in the basin and more severe in western Africa than in the Congo Basin (Laurance 1999). To better approximate reality, some investigators modelled actual (*ca.* 1988) deforestation patterns in Brazilian Amazonia. Predicted effects have been less dramatic than for uniform clearing, with deforested regions experiencing limited (6–8%) declines in rainfall, moderate (18–33%) reductions in evapotranspiration, elevated surface temperatures and greater wind speeds (owing to reduced surface drag) that could affect moisture convergence and circulation (Walker *et al.* 1995; Sud *et al.*

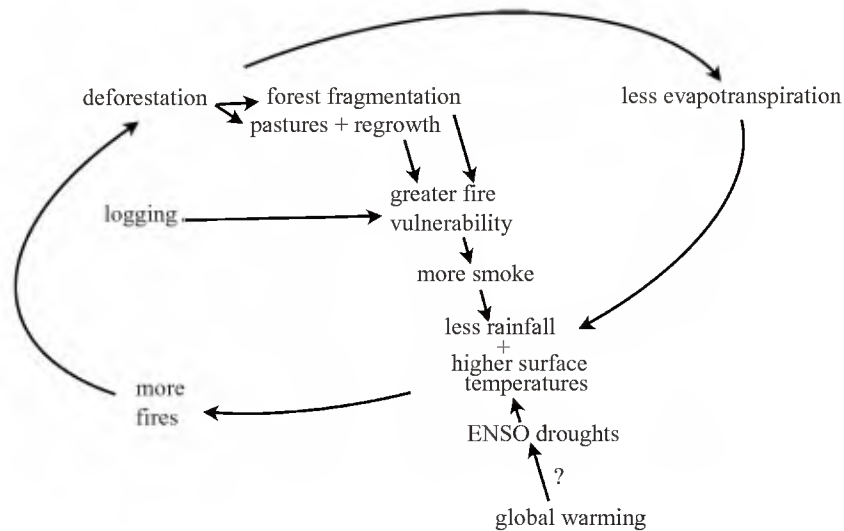


Figure 5. Potential positive feedbacks among forest fragmentation, logging, fires and climate change in the Amazon (after Laurance & Williamson 2001).

1996). Although of limited magnitude, for the large expanses of Amazonia that have pronounced dry seasons and are strongly influenced by El Niño droughts (Nepstad *et al.* 1994), even modest drying and warming trends could potentially cause marked increases in forest vulnerability to fire, especially where forests are fragmented or logged.

Forest clearing and fragmentation create mosaics of land with different physical properties. One potentially important effect of increasing fragmentation is the 'vegetation breeze', whereby moist air is pulled away from forests into adjoining pastures and clearings (e.g. Silva Dias & Regnier 1996; Baidya Roy & Avissar 2000). The humid air over forests is drawn into the clearing and condenses into rain-producing clouds, then is recycled—as dry air—back over the forest. This effect has been observed in clearings as small as a few hundred hectares, but extensive clearings spanning *ca.* 100 km or more apparently cause much larger-scale forest desiccation (Avissar & Liu 1996). In Rondônia, Brazil, Silva Dias *et al.* (2002) describe a 20 km wide zone of reduced rainfall surrounding large forest clearings. Thus, by drawing moisture away from adjoining forests, large clearings might increase the vulnerability of forests to fire.

The deforestation process itself can also increase forest desiccation. Smoke from tropical forest fires has been shown to reduce rainfall and possibly cloud cover (Rosenfeld 1999). This occurs because burning hypersaturates the atmosphere with cloud condensation nuclei (microscopic particles in aerosol form) that bind with water molecules in the atmosphere, inhibiting the formation of raindrops. As a result, large-scale forest burning can create rain shadows that have been observed to extend for hundreds of kilometres downwind (Freitas *et al.* 2000). Aerosols from forest burning may also affect the thermodynamic stability of the atmosphere, by absorbing and scattering incoming solar radiation and increasing cloud formation, but the consequences of such changes are poorly understood (Martins *et al.* 1998; Andreae 2001).

The diverse environmental changes that affect cleared and fragmented landscapes might interact in complex ways. Of particular concern is that positive feedbacks may arise (figure 5), in which large-scale deforestation increases

local or regional desiccation and thereby renders remaining forests more vulnerable to fire, promoting further deforestation (Laurance & Williamson 2001; Nepstad *et al.* 2001). Such feedbacks could be driven by many of the mechanisms described above—edge-related fires, the vegetation breeze, the moisture-trapping effects of smoke plumes and regional drying and warming from declining evapotranspiration, among others. The net effect is that large expanses of forest that are currently too humid or intact to burn readily may become more vulnerable in the future. Such changes could profoundly influence the rate and spatial pattern of forest destruction; for example, more seasonal forests often face considerably higher conversion pressure than wetter forests, because the former are both easier to burn initially and require less effort to maintain as pastures and farms (Schneider *et al.* 2000; Laurance *et al.* 2002b). A greater incidence of fire in the tropics could also have important global effects, by increasing greenhouse-gas emissions and thereby exacerbating global warming (Fearnside 2000; Houghton *et al.* 2000).

7. LARGER-SCALE EFFECTS

In addition to local and regional effects, tropical deforestation could have important remote impacts on other regions. In Costa Rica, for example, extensive deforestation of the nearby Caribbean lowlands has apparently led to marked downwind reductions of cloud cover, rainfall and mist at Monteverde Cloud Forest Reserve (Lawton *et al.* 2001). Modelling studies suggest that rapidly increasing deforestation in the Indonesian Archipelago may have a strong impact on the broader regional climate due to feedbacks among the biosphere, atmosphere and ocean (Delire *et al.* 2001). Some simulations suggest that heavy Amazonian deforestation will alter precipitation in areas south of the basin (Henderson-Sellers *et al.* 1993), in Central America and the Caribbean, and even at middle and higher latitudes (Gandú & Silva Dias 1998; Gedney & Valdes 2000; Avissar & Nobre 2002; Avissar *et al.* 2002).

Finally, the regional climatic effects of deforestation could potentially interact with global warming. Costa & Foley

(2000) concluded that global warming would exacerbate the effects of Amazonian deforestation, which by reducing evapotranspiration limits the capacity of the land surface to cool itself. The net effect could be markedly higher surface temperatures and a 20% reduction in regional rainfall (Costa & Foley 2000). In addition, some models suggest that El Niño droughts and tropical storms may increase in frequency or severity as a result of global warming (IPCC 1996; Timmermann 1999). At the least, the frequency of warm weather events should rise and the likelihood of cool weather events decline, because of higher mean temperatures (Mahlman 1997). Thus, by increasing the incidence of droughts and hot weather, global warming could potentially promote alarming positive feedbacks among deforestation, regional desiccation and fire (figure 5).

8. CONCLUSIONS

A great deal remains unknown about the influence of land-cover change on tropical forest–climate interactions. Local-scale processes have been best characterized, but important questions remain. For example, virtually nothing is known about the effects of altered microclimatic conditions near forest edges on plant and soil respiration rates (cf. Nascimento & Laurance 2004). Higher temperatures near edges should generally increase respiration, whereas reduced humidity near edges could have an opposite effect (e.g. Chambers *et al.* 2000, 2001). Given that tropical soils contain more carbon (in soil organic matter and root biomass) than the above-ground vegetation (Davidson & Trumbore 1995; Moraes *et al.* 1995), altered soil respiration rates could potentially have a large impact on the carbon balance of fragmented forests. On larger scales, our understanding of the effects of deforestation on regional climates is still rudimentary, despite many indications that such effects will be deleterious to forests.

For those attempting to assess the effects of global-change phenomena on intact tropical forests, it must be emphasized that edge-related alterations could penetrate large distances into forest tracts. Diverse physical and biotic changes often occur within the first 100–300 m of edges, and other phenomena, such as surface fires, may penetrate up to several kilometres inside forest margins. Where forest tracts adjoin major clearings, alterations in atmospheric circulation might infiltrate even farther into forests, perhaps 20 km or more. Given the rapid pace of forest conversion in the tropics, care must be taken to distinguish the consequences of global-change phenomena from the ever-increasing effects of landscape alteration.

The author thanks Pedro Silva Dias, Roni Avissar, Valerie Kapos, Carlos Peres, Aurélie Botta and Yadvinder Malhi for commenting on drafts of the paper. Research support was provided by the NASA-LBA program, Conservation, Food and Health Foundation, and A. W. Mellon Foundation. This is publication number 403 in the BDFFP technical series.

REFERENCES

- Achard, F., Eva, H. D., Stibig, H.-J., Mayaux, P., Gallego, J., Richards, T. & Malingreau, J.-P. 2002 Determination of deforestation rates of the world's humid tropical forests. *Science* **297**, 999–1002.
- Andrae, M. 2001 The dark side of aerosols. *Nature* **409**, 671–672.
- Avissar, R. & Liu, Y. 1996 A three-dimensional numerical study of shallow convective clouds and precipitation induced by land-surface forcing. *J. Geophys. Res.* **101**, 7499–7518.
- Avissar, R. & Nobre, C. A. 2002 The Large-Scale Biosphere–Atmosphere Experiment in Amazonia (LBA). *J. Geophys. Res.* **107**, 8034. (DOI 10.1029/2002JD002507.)
- Avissar, R., Silva Dias, P. L., Silva Dias, M. A. F. & Nobre, C. A. 2002 The Large-Scale Biosphere–Atmosphere Experiment in Amazonia (LBA): Insights and future research needs. *J. Geophys. Res.* **107**, 8086. (DOI 10.1029/2002JD002704.)
- Baidya Roy, S. & Avissar, R. 2000 Scales of response of the convective boundary layer to land-surface heterogeneity. *Geophys. Res. Lett.* **27**, 533–536.
- Barlow, J. & Peres, C. A. 2004 Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. *Phil. Trans. R. Soc. Lond. B* **359**, 367–380. (DOI 10.1098/rstb.2003.1423.)
- Barlow, J., Peres, C. A., Lagan, B. O. & Haugaasen, T. 2003 Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecol. Lett.* **6**, 6–8.
- Bergen, J. D. 1985 Some estimates of dissipation from the turbulent velocity component gradients over a forest canopy. In *The forest–atmosphere interaction* (ed. B. A. Hutchinson & B. B. Hicks), pp. 613–630. Dordrecht, The Netherlands: D. Reidel.
- Bruna, E. M. 1999 Seed germination in rainforest fragments. *Nature* **402**, 139.
- Bruna, E. M. 2002 Experimental assessment of *Heliconia acuminata* growth in a fragmented Amazonian landscape. *J. Ecol.* **90**, 639–649.
- Bull, G. A. D. & Reynolds, E. 1968 Wind turbulence generated by vegetation and its implications. *Forestry* **41**, 28–37.
- Camargo, J. L. C. & Kapos, V. 1995 Complex edge effects on soil moisture and microclimate in central Amazonian forest. *J. Trop. Ecol.* **11**, 205–211.
- Carvalho, K. S. & Vasconcelos, H. L. 1999 Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biol. Conserv.* **91**, 151–158.
- Chambers, J. Q., Higuchi, N., Schimel, J. P., Ferreira, L. V. & Melack, J. M. 2000 Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* **122**, 380–388.
- Chambers, J. Q., Schimel, J. P. & Nobre, A. D. 2001 Respiration from coarse wood litter in central Amazon forests. *Biogeochemistry* **52**, 115–131.
- Cochrane, M. A. 2001 In the line of fire: understanding the dynamics of tropical forest fires. *Environment* **43**, 28–38.
- Cochrane, M. A. & Laurance, W. F. 2002 Fire as a large-scale edge effect in Amazonian forests. *J. Trop. Ecol.* **18**, 311–325.
- Cochrane, M. A. & Schulze, M. D. 1999 Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. *Biotropica* **31**, 2–16.
- Cochrane, M. A., Alencar, A., Schulze, M. D., Souza, C., Nepstad, D., Lefebvre, P. & Davidson, E. 1999 Positive feedbacks in the fire dynamics of closed canopy tropical forests. *Science* **284**, 1832–1835.
- Costa, M. & Foley, J. 2000 Combined effects of deforestation and doubled atmospheric CO₂ concentrations on the climate of Amazonia. *J. Climat.* **13**, 18–34.
- Curran, L. M., Caniago, I., Paoli, G., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C. & Haeruman, H. 1999 Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* **286**, 2184–2188.

- D'Angelo, A., Andrade, A., Laurance, S. G. & Laurance, W. F. 2002 Patterns of tree mortality and damage in fragmented and intact forests of central Amazonia. Poster presentation, *Ann. Conf. Long-term Biosphere–Atmosphere Experiment in the Amazon (LBA) Program, Manaus, Brazil*.
- Davidson, E. A. & Trumbore, S. E. 1995 Gas diffusivity and the production of CO₂ in deep soils of the eastern Amazon. *Tellus B* **47**, 550–565.
- Delire, C., Behling, P., Coe, M. T., Foley, J. A., Jacob, R., Kutzbach, J., Liu, Z. & Vavrus, L. 2001 Simulated response of the atmosphere–ocean system to deforestation in the Indonesian archipelago. *Geophys. Res. Lett.* **28**, 2081–2084.
- Dickinson, R. & Kennedy, P. 1992 Impacts on regional climate of Amazon deforestation. *Geophys. Res. Lett.* **19**, 1947–1950.
- Didham, R. K. & Lawton, J. H. 1999 Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* **31**, 17–30.
- Fearnside, P. M. 2000 Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Climat. Change* **46**, 115–158.
- Ferreira, L. V. & Laurance, W. F. 1997 Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. *Conserv. Biol.* **11**, 797–801.
- Freitas, S. R., Silva Dias, M. A. F. & Silva Dias, P. L. 2000 Modeling the convective transport of trace gases by deep and moist convection. *Hydrol. Meth. Engng* **3**, 317–330.
- Gandú, A. W. & Silva Dias, P. L. 1998 Impact of tropical heat sources on the South American tropospheric upper circulation and subsidence. *J. Geophys. Res.* **103**, 6001–6015.
- Gascon, C., Williamson, G. B. & Fonseca, G. A. B. 2000 Receding edges and vanishing reserves. *Science* **288**, 1356–1358.
- Gash, J. H. C. & Nobre, C. A. 1997 Climatic effects of Amazonian deforestation: some results from ABRACOS. *Bull. Am. Meteorol. Soc.* **78**, 823–830.
- Gedney, N. & Valdes, P. J. 2000 The effect of Amazonian deforestation on the northern hemisphere circulation and climate. *Geophys. Res. Lett.* **27**, 3053–3056.
- Gudhardja, E., Fatawi, M., Sutisna, M., Mori, T. & Ohta, S. 2000 Rainforest ecosystems of East Kalimantan: El Niño, drought, fire and human impacts. *Ecol. Stud.* **140**, 1–330.
- Henderson-Sellers, A., Dickinson, R., Durbridge, T., Kennedy, P., McGuffie, K. & Pitman, A. 1993 Tropical deforestation: modeling local to regional scale climate change. *J. Geophys. Res.* **98**, 7289–7315.
- Holdsworth, A. R. & Uhl, C. 1997 Fire in Amazonian selectively logged rain forest and the potential for fire reduction. *Ecol. Applic.* **7**, 713–725.
- Houghton, R. A., Skole, D. L., Nobre, C. A., Hackler, J. L., Lawrence, K. T. & Chomentowski, W. H. 2000 Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature* **403**, 301–304.
- IPCC 1996 *Climate change 1995: impacts, adaptations and mitigation of climate change: scientific technical analyses*. Intergovernmental Panel on Climate Change. Cambridge University Press.
- Kapos, V. 1989 Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* **5**, 173–185.
- Kapos, V., Ganade, G., Matsui, E. & Victoria, R. L. 1993 $\alpha^{13}\text{C}$ as an indicator of edge effects in tropical rainforest reserves. *J. Ecol.* **81**, 425–432.
- Kauffman, J. B., Cummings, D. L., Ward, D. E. & Babbitt, R. 1995 Fire in the Brazilian Amazon: biomass, nutrient pools, and losses and slashed primary forests. *Oecologia* **104**, 397–408.
- Kinnaird, M. F. & O'Brien, T. G. 1998 Ecological effects of wildfire on lowland rainforest in Sumatra. *Conserv. Biol.* **12**, 954–956.
- Lanly, J. P. 1982 Tropical forest resources. FAO Forestry paper 30. Rome: United Nations Food and Agricultural Organization.
- Laurance, W. F. 1997 Hyper-disturbed parks: edge effects and the ecology of isolated rainforest reserves in tropical Australia. In *Tropical forest remnants: ecology, management, and conservation of fragmented communities* (ed. W. F. Laurance & R. O. Bierregaard), pp. 71–83. University of Chicago Press.
- Laurance, W. F. 1999 Reflections on the tropical deforestation crisis. *Biol. Conserv.* **91**, 109–117.
- Laurance, W. F. & Bierregaard, R. O. 1997 *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press.
- Laurance, W. F. & Cochrane, M. A. 2001 Synergistic effects in fragmented landscapes. *Conserv. Biol.* **15**, 1488–1489.
- Laurance, W. F. & Williamson, G. B. 2001 Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conserv. Biol.* **15**, 1529–1535.
- Laurance, W. F., Laurance, S. G., Ferreira, L. V., Rankin-de Merona, J., Gascon, C. & Lovejoy, T. E. 1997 Biomass collapse in Amazonian forest fragments. *Science* **278**, 1117–1118.
- Laurance, W. F., Ferreira, L. V., Rankin-de Merona, J. & Laurance, S. G. 1998a Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* **79**, 2032–2040.
- Laurance, W. F., Ferreira, L. V., Rankin-de Merona, J., Laurance, S. G., Hutchings, R. & Lovejoy, T. E. 1998b Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conserv. Biol.* **12**, 460–464.
- Laurance, W. F., Laurance, S. G. & Delamonica, P. 1998c Tropical forest fragmentation and greenhouse gas emissions. *Forest. Ecol. Mngmt* **110**, 173–180.
- Laurance, W. F., Delamonica, P., Laurance, S. G., Vasconcelos, H. & Lovejoy, T. E. 2000 Rainforest fragmentation kills big trees. *Nature* **404**, 836.
- Laurance, W. F., Perez-Salicrup, D., Delamonica, P., Fearnside, P., D'Angelo, S., Jerozolinski, A., Pohl, L. & Lovejoy, T. E. 2001 Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **82**, 105–116.
- Laurance, W. F., Albernaz, A. K. M., Schroth, G., Fearnside, P. M., Ventincinque, E. & Da Costa, C. 2002a Predictors of deforestation in the Brazilian Amazon. *J. Biogeogr.* **29**, 737–748.
- Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E., Didham, R., Stouffer, P., Gascon, C., Bierregaard, R., Laurance, S. & Sampaio, E. 2002b Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* **16**, 605–618.
- Lawton, R. O., Nair, U. S., Pielke, S. A. & Welch, R. M. 2001 Climatic impact of lowland deforestation on nearby montane cloud forests. *Science* **294**, 584–587.
- Lean, J. & Rowntree, P. R. 1993 A GCM simulation of the impact of Amazonian deforestation on climate using an improved canopy representation. *Q. J. R. Meteorol. Soc.* **119**, 509–530.
- Lean, J. & Warrilow, D. 1989 Climatic impact of Amazon deforestation. *Nature* **342**, 311–313.
- Leighton, M. & Wirawan, N. 1986 Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982–1983 El Niño–Southern Oscillation event. In *Tropical rain forests and the world atmosphere* (ed. G. T. Prance), pp. 75–102. Boulder, CO: AAAS Symposium 10.
- Lewis, S. 1998 Treefall gaps and regeneration: a comparison of continuous forest and fragmented forest in central Amazonia. PhD thesis, University of Cambridge, UK.
- Lovejoy, T. E. (and 10 others) 1986 Edge and other effects of isolation on Amazon forest fragments. In *Conservation biology: the science of scarcity and diversity* (ed. M. E. Soulé), pp. 257–285. Sunderland, MA: Sinauer.

- Lugo, A. E., Applefield, M., Pool, D. & McDonald, R. 1983 The impact of Hurricane David on the forests of Dominica. *Can. J. Forest Res.* **132**, 201–211.
- Mahlman, J. D. 1997 Uncertainties in projections of human-caused climate warming. *Science* **278**, 1416–1417.
- Malcolm, J. R. 1994 Edge effects in central Amazonian forest fragments. *Ecology* **75**, 2438–2445.
- Malcolm, J. R. 1998 A model of conductive heat flow in forest edges and fragmented landscapes. *Climat. Change* **39**, 487–502.
- Martins, J. V., Artaxo, P., Liousse, C., Reid, J., Hobbs, P. & Kaufman, Y. 1998 Effects of black carbon content, particle size and mixing on light absorption by aerosol particles from biomass burning in Brazil. *J. Geophys. Res.* **103**, 32 041–32 050.
- Mesquita, R., Delamonica, P. & Laurance, W. F. 1999 Effects of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biol. Conserv.* **91**, 129–134.
- Miller, D. R., Lin, J. D. & Lu, Z. 1991 Some effects of surrounding forest canopy architecture on the wind field in small clearings. *Forest. Ecol. Mgmt* **45**, 79–91.
- Moraes, J. L., Cerri, C. C., Mellilo, J., Kicklighter, D., Neill, C., Skole, D. & Steudler, P. 1995 Soil carbon stocks of the Brazilian Amazon basin. *J. Am. Soil Sci. Soc.* **59**, 244–247.
- Nascimento, H. E. M. & Laurance, W. F. 2004 Biomass dynamics in Amazonian forest fragments. *Ecol. Applic.* (In the press.)
- Nelson, B. W., Kapos, V., Adams, J., Oliveira, W., Braun, O. & do Amaral, I. 1994 Forest disturbance by large blow-downs in the Brazilian Amazon. *Ecology* **75**, 853–858.
- Nepstad, D. C., Carvalho, C., Davidson, E., Jipp, P., Lefebvre, P., Negreiros, P., Silva, E., Stone, T., Trumbore, S. & Viera, S. 1994 The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **372**, 666–669.
- Nepstad, D. C., Moreira, A. G. & Alencar, A. A. 1999 *Flames in the rain forest: origins, impacts, and alternatives to Amazonian fires*. Brasilia, Brazil: Pilot Program to Preserve the Brazilian Rain Forest.
- Nepstad, D. C., Carvalho, G., Barros, A. C., Alencar, A., Capobianco, J. P., Bishop, J., Moutinho, P., Lefebvre, P., Silva, U. L. & Prins, E. 2001 Road paving, fire regime feedbacks, and the future of Amazonian forests. *Forest. Ecol. Mgmt* **154**, 395–407.
- Nobre, C. A., Sellers, P. J. & Shukla, J. 1991 Amazonian deforestation and regional climate change. *J. Climat.* **4**, 411–413.
- Oliveira-Filho, A. T., de Mello, J. & Scolforo, J. 1997 Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987–1992). *Pl. Ecol.* **131**, 45–66.
- Peres, C. A. 1999 Ground fires as agents of mortality in a central Amazonian forest. *J. Trop. Ecol.* **15**, 535–541.
- Ranta, P., Blom, T., Niemela, J., Joensuu, E. & Siitonen, M. 1998 The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. *Biodivers. Conserv.* **7**, 385–403.
- Reville, B. J., Tranter, J. D. & Yorkston, H. D. 1990 Impacts of forest clearing on the endangered seabird *Sula abbottii*. *Biol. Conserv.* **51**, 23–38.
- Rosenfeld, D. 1999 TRMM observed first direct evidence of smoke from forest fires inhibiting rainfall. *Geophys. Res. Lett.* **26**, 3105–3108.
- Savill, P. S. 1983 Silviculture in windy climates. *Forest. Abstr.* **44**, 473–488.
- Scariot, A. 2001 Seedling mortality by litterfall in Amazonian forest fragments. *Biotropica* **32**, 662–669.
- Schneider, R. R., Arima, E., Verissimo, A., Barreto, P. & Souza Jr, C. 2000 *Amazônia sustentável: limitantes e oportunidades para o desenvolvimento rural*. Brasilia, Brazil: The World Bank.
- Siegert, F., Ruecker, G., Hinrichs, A. & Hoffmann, A. A. 2001 Increased damage from fires in logged forests during droughts caused by El Niño. *Nature* **414**, 437–440.
- Silva Dias, P. L. & Regnier, P. 1996 Simulation of mesoscale circulations in a deforested area of Rondônia in the dry season. In *Amazonian deforestation and climate* (ed. J. Gash, C. Nobre, J. Roberts & R. Victoria), pp. 531–547. San Francisco, CA: Wiley.
- Silva Dias, M. A. F., Williams, E., Pereira, L., Pereira Filho, A. & Matsuo, P. 2002 A case study of convective organization into precipitating lines in the Southwest Amazon during the WETAMC and TRMM-LBA. *J. Geophys. Res.* **107**, 8078. (DOI 10.1029/2001JD000375.)
- Sizer, N. & Tanner, E. V. J. 1999 Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biol. Conserv.* **91**, 135–142.
- Sizer, N. C., Tanner, E. V. J. & Kossman Ferraz, I. D. 2000 Edge effects on litterfall mass and nutrient concentrations in forest fragments in central Amazonia. *J. Trop. Ecol.* **16**, 853–863.
- Skole, D. & Tucker, C. J. 1993 Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* **260**, 1905–1910.
- Somerville, A. 1980 Wind stability: forest layout and silviculture. *NZ J. Forest. Sci.* **10**, 476–501.
- Sud, Y., Yang, R. & Walker, G. 1996 Impact of *in situ* deforestation in Amazonia on the regional climate: general circulation model simulation study. *J. Geophys. Res.* **101**, 7095–7109.
- Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. & Roeckner, E. 1999 Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* **398**, 694–697.
- Turton, S. M. 1992 Understorey light environments in a north-east Australian rain forest before and after a tropical cyclone. *J. Trop. Ecol.* **8**, 241–252.
- Turton, S. M. & Freiburger, H. J. 1997 Edge and aspect effects on the microclimate of a small tropical forest remnant on the Atherton Tableland, northeastern Australia. In *Tropical forest remnants: ecology, management, and conservation of fragmented communities* (ed. W. F. Laurance & R. O. Bierregaard), pp. 45–54. University of Chicago Press.
- Uhl, C. & Kauffman, J. B. 1990 Deforestation effects on fire susceptibility and the potential response of the tree species to fire in the rainforest of the eastern Amazon. *Ecology* **71**, 437–449.
- Viana, V. M., Tabanez, A. A. & Batista, J. 1997 Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. In *Tropical forest remnants: ecology, management, and conservation of fragmented communities* (ed. W. F. Laurance & R. O. Bierregaard), pp. 352–365. University of Chicago Press.
- Walker, G. K., Sud, Y. C. & Atlas, R. 1995 Impact of ongoing Amazonian deforestation on local precipitation: a GCM simulation study. *Bull. Am. Meteorol. Soc.* **76**, 346–361.
- Weathers, K. C., Cadenasso, M. L. & Pickett, S. T. A. 2001 Forest edges as nutrient and pollution concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conserv. Biol.* **15**, 1506–1514.
- Webb, L. J. 1958 Cyclones as an ecological factor in tropical lowland rain forest, North Queensland. *Aust. J. Bot.* **6**, 220–228.
- Whitmore, T. C. 1975 *Tropical rain forests of the Far East*. Oxford: Clarendon.
- Wright, I. R., Gash, J. H. C., da Rocha, H. R. & Roberts, J. M. 1996 Modelling surface conductance for Amazonian pasture and forest. In *Amazonian deforestation and climate* (ed. J. H. C. Gash, C. A. Nobre, J. M. Roberts & R. L. Victoria), pp. 438–458. San Francisco, CA: Wiley.