CHAPTER 3

Forest–climate interactions in fragmented tropical landscapes

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In the tropics, habitat fragmentation alters forest–climate interactions in diverse ways. On a local scale (<1 km), elevated desiccation and wind disturbance near fragment margins lead to sharply increased tree mortality, 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.

Introduction

The fragmented landscape is becoming one of the most ubiquitous 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 last 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 and Bierregaard 1997) and alter many ecosystem functions such as carbon storage, biogeochemical cycling, and regional hydrology (Lean and Warrilow 1989; Kauffman *et al.* 1995; Fearnside 2000).

Here I synthesize 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.

Size and shape of fragments

The processes of deforestation and forest fragmentation are inextricably linked. As land conversion proceeds, remnant forest patches almost always persist (by happenstance 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 (<100 ha) forest fragments (Fig. 3.1), although a sizeable fraction of the remaining forest may persist in a few large (>1000 ha) fragments (Ranta *et al.* 1998; Gascon *et al.* 2000; Cochrane and 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 (Fig. 3.2). In the Brazilian Amazon, for example, the area of forest in 1988 that was fragmented (<100 km^2 in area) or vulnerable to edge effects (<1 km from forest edge) was over 150% larger than that which had actually been deforested (Skole and 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 (M. A. Cochrane, personal communication).

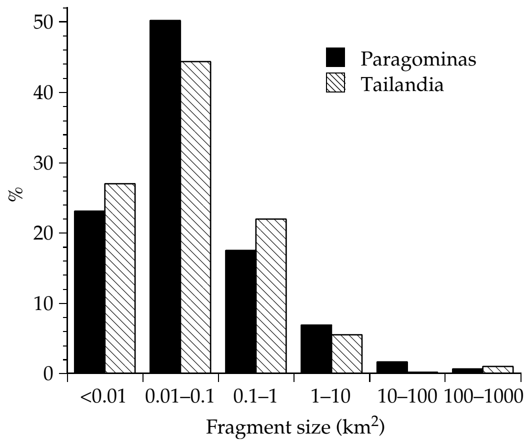

Figure 3.1 In human-dominated landscapes, most forest fragments are small (<1 km^2). Data shown are for two fragmented areas in eastern Amazonia (after Cochrane and Laurance 2002).

Microclimate and wind

On a local scale (<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 and 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 nearly continuous canopy cover (Lovejoy *et al.* 1986; Laurance *et al.* 2002a), but when adjoined by clearings these conditions are sharply altered. On newly created edges, elevated temperatures, reduced humidity, and increased sunlight and vapour pressure deficits can penetrate

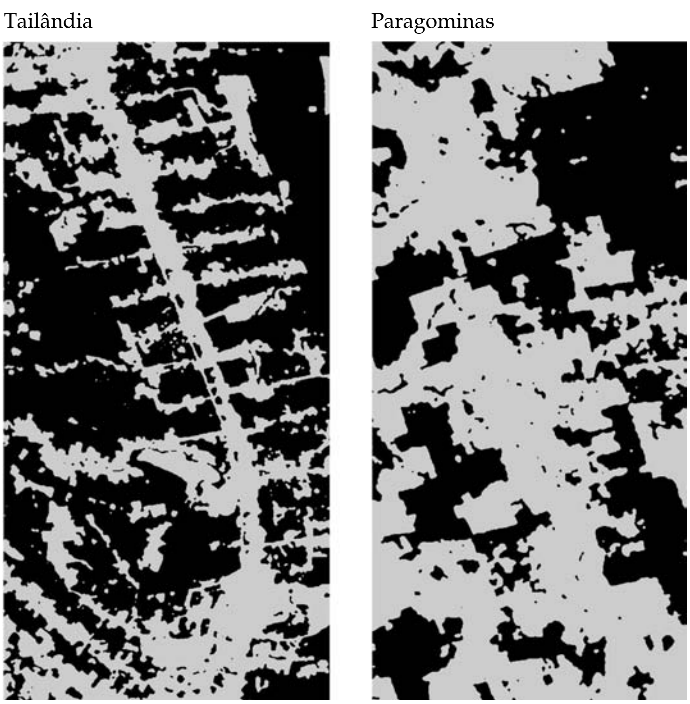

Figure 3.2 Habitat fragmentation leads to a proliferation of forest edge, as shown in two landscapes in eastern Amazonia (each 600 km^2 in area; dark areas are forest and light areas are mostly pastures). Tailândia, a government-sponsored colonization project, shows the characteristic 'fish-bone' pattern of deforestation, whereas 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 and Laurance 2002).

at least 40–60 m into fragment interiors (Kapos 1989; Didham and Lawton 1999; Sizer and Tanner 1999). Such changes increase evapotranspiration in understorey 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 increased 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 about 7° to 20° latitude (Webb 1958; Lugo *et al.* 1983), and also in equatorial forests affected by convectional 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). Greater windspeeds increase the persistence and frequency of wind eddies near edges that can heavily buffet the upper 40% of the forest (Bull and Reynolds 1968).

These physical alterations lead to sharply increased tree mortality and damage within 100–300 m of fragment margins (Fig. 3.3; Laurance *et al.* 1998a). In central Amazonia, large (>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 and 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.* 2004).

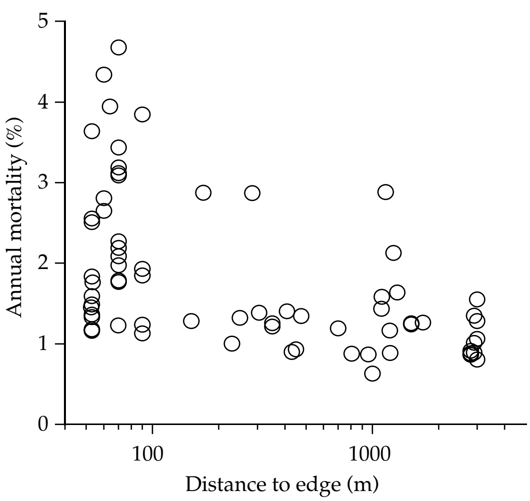

Figure 3.3 In rainforests, tree mortality rises sharply near forest edges. Data shown are from a long-term experimental study of forest fragmentation in the central Amazon (after Laurance *et al.* 1998a).

Chronically elevated tree mortality has myriad effects. It fundamentally alters canopy-gap dynamics (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 towards 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.* 2001b). Leaf litter accumulates near edges (Sizer *et al.* 2000; Vasconcelos and Luizão 2004) 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 and Laurance 2004), and are probably a non-trivial source of atmospheric carbon emissions (Laurance *et al.* 1998c).

Accelerated tree mortality directly affects forest–climate interactions by increasing the density of treefall gaps and altering canopy structure. Recurring canopy damage exacerbates edge-related changes in microclimate, increasing daytime temperature (Malcolm 1998) and vapour pressure deficits (Camargo and 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 and Reynolds 1968) 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.

Edge and landscape structure

The physical structure of edges strongly influences forest–climate interactions. In the tropics, newly formed edges (<5 yr 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 and Kapos 1995; Didham and 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 and Lawton 1999; Gascon *et al.* 2000).

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

Edge-related fires

Except when subjected to strong droughts (Leighton and Wirawan 1986; Peres 1999; Gudhardja *et al.* 2000), 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.* 1999a). 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 and Laurance 2004; Vasconcelos and Luizão 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 and Williamson 2001) and thereby augment forest fuels at a time when conditions are driest. Finally, forest fragments are frequently disturbed by logging (Laurance and Cochrane 2001), which further exacerbates forest desiccation, fuel loading, and vulnerability to fire (Uhl and Kauffman 1990; Holdsworth and Uhl 1997; Siegert *et al.* 2001).

In the eastern Amazon, surface fires that originate in adjoining pastures can penetrate large distances into fragment interiors (Fig. 3.4; Cochrane and 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 and Kauffman 1990). Even light fires kill up to half of all trees and virtually all vines (Cochrane and Schulze 1999; Barlow *et al.* 2003). 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 (>100,000 ha) forest fragments may be vulnerable (Cochrane and Laurance 2002).

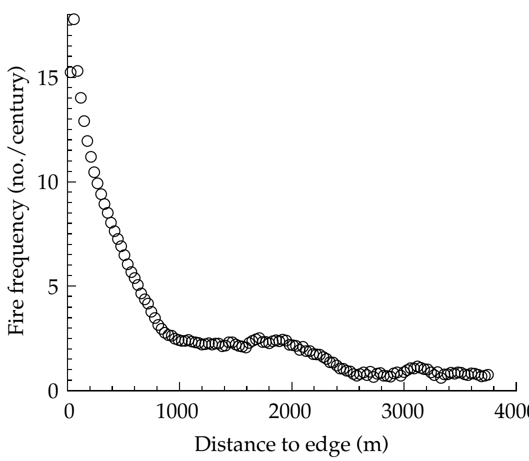

Figure 3.4 Estimated fire frequencies as a function of distance from forest edge for the Tailândia region in eastern Amazonia. Data are based on remote-sensing imagery spanning a 14-yr period (after Cochrane and Laurance 2002).

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 those occurring during El Niño events throughout large areas of the neotropics, Southeast Asia, and Australasia (Leighton and Wirawan 1986; Kinnaird and O'Brien 1998; Cochrane *et al.* 1999; Curran *et al.* 1999; Nepstad *et al.* 1999a; Barlow *et al.* 2003). 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 ha (13% of the total forest area) may already be vulnerable to edge-related fires (Cochrane 2001).

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 meso-scale 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 here 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 (Nobre *et al.* 1991; Dickinson and Kennedy 1992; Lean and Rowntree 1993; Gash and Nobre 1997) or Southeast Asian (Henderson-Sellers *et al.* 1993) forests to pasture or savanna. Although results have varied, most studies predict that uniform deforestation will lead to markedly decreased regional rainfall (on the order of 20–30%) as well as lower evaporation, cloud cover, and soil moisture; and higher albedo and surface temperatures (Lean and Rowntree 1993; Sud *et al*. 1996; Gash and Nobre 1997).

However, regional patterns of forest loss are never uniform. For example, tropical deforestation is much greater in south-eastern 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 (due to reduced surface drag) that could affect moisture convergence and circulation (Walker *et al.* 1995; Sud *et al.* 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 (Silva Dias and Regnier 1996; Baidya Roy and 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 roughly 100 km or more apparently cause much larger-scale forest desiccation (Avissar and 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 altering cloud formation, but the consequences of such changes for the regional hydrology and climate are poorly understood (Martins *et al.* 1998; Andreae 2001). During the dry season, large expanses of the Amazon (ca. 1.2–2.6 million km^2) exhibit significantly elevated levels of atmospheric aerosols from forest burning (Procopio *et al.* 2004).

The diverse environmental changes that affect cleared and fragmented landscapes might interact in complex ways. Of particular concern is that positive feedbacks may arise (Fig. 3.5), in which large-scale deforestation increases local or regional desiccation and thereby renders remaining forests more vulnerable to fire, promoting further deforestation (Laurance and 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).

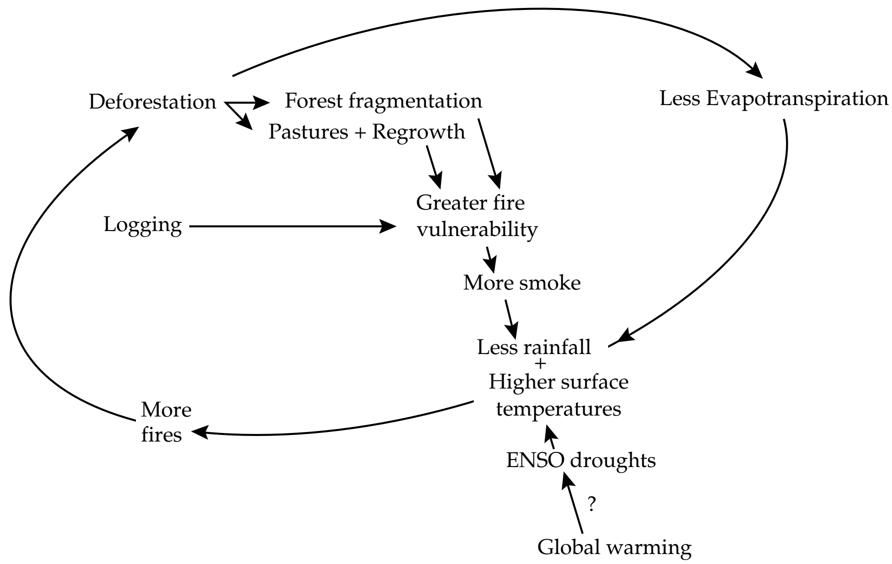

Figure 3.5 Potential positive feedbacks among forest fragmentation, logging, fires, and climate change in the Amazon (after Laurance and Williamson 2001).

Larger-scale effects

In addition to local and regional effects, tropical deforestation could have important remote impacts on other regions. In Costa Rica, 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 as a result of 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 and Silva Dias 1998; Gedney and Valdez 2000; Avissar and Nobre 2002; Avissar *et al.* 2002).

Finally, the regional climatic effects of deforestation could potentially interact with global warming. Costa and 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 and 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; Timmerman *et al.* 1999). At the least, the frequency of warm weather events should rise, and the likelihood of cool weather events should decline, as a consequence 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 (Fig. 3.5).

Conclusions

Much 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.

Higher temperatures near edges should generally increase respiration whereas reduced humidity near edges could have an opposite effect (e.g. Chambers *et al.* 2001d). Given that tropical soils contain more carbon (in soil organic matter and root biomass) than the above-ground vegetation (Davidson and 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 can 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. Finally, markedly increased concentrations of atmospheric aerosols, which have poorly understood effects on cloud cover and atmospheric stability, can occur up to several hundred kilometers downwind of major areas of biomass burning. 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- and region-scale alterations.