Carbon Dynamics of Tropical Forests

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Executive Summary

Tropical forests, a critical resource affecting world climate, are very diverse, largely because of variations in regional climate and soil. For purposes of this analysis they have been divided in four broad forest types – ever-wet, semi-evergreen, dry deciduous, and montane. Existing literature on climate and tropical forests suggests that, compared to temperate and boreal forest biomes, tropical forests play a disproportionate role in contributing to emissions that both affect and mitigate climate. This chapter describes the geographical extent of tropical forests and their role in terrestrial carbon storage, uptake (through processes of photosynthesis), and loss (through plant respiration and microbial decomposition of dead biomass). A review is provided of current knowledge about the role of disturbance (natural and human caused) in affecting the carbon balance of tropical forests. The chapter concludes with an analysis of the threats to tropical forests and how they may influence climate change and elevated CO_2. Findings of this review are summarized in the section below under "what we know" and "what we don't know" about the carbon dynamics of tropical forests.

What We Do Know About Carbon Storage and Flux in Tropical Forests

- Tropical forests contribute nearly half of the total terrestrial gross primary productivity. About 8% of the total atmospheric carbon dioxide cycles through these forests annually.
- Tropical forests contain about 40% of the stored carbon in the terrestrial biosphere (estimated at 428 Gt of carbon), with vegetation accounting for 58% and soil 41%. This ratio of vegetation carbon to soil carbon varies greatly by tropical forest type.
- If tropical ever-wet forest soils become drier, the few studies that have been done suggest that litter decomposition and release of CO_2 from soil may slow. However, some studies show that release of methane, which has a higher global warming potential than CO_2, increases as soils dry. The cause of the methane increase is suspected to be related to increased termite activity.
- Tropical ever-wet and semi-evergreen forests in the Amazon and southeastern Asia typically suffer from droughts during ENSO events (El Niño – La Niña). In the short-term, tropical forests may be resilient to drought. However,

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this may be offset by increased vulnerability to fire after both short- and long-term droughts. These droughts are more severe during strong El Niño years. In tropical ever-wet forests, where droughts are rare, mortality may increase during strong El Niño years due to severe drought, while seasonal semi-evergreen forests may experience relatively little change.
- Expanding crop and pasture lands have a profound effect on the global carbon cycle as tropical forests typically store 20–100 times more carbon per unit area than the agriculture that replaces them. The use of fire to clear forested lands may exacerbate changes to carbon cycling since fire fills the atmosphere with aerosols, thereby reducing transpiration.
- There are proportionately higher amounts of fine root biomass (as compared to other vegetative parts – e.g. leaves, stem) in infertile soils as compared to fertile soils. Infertile soils (e.g. oxisols) make up a greater proportion of the African and South American upland ever-wet and semi-evergreen forest than any other soil type.
- CO_2 production in tropical soils is positively correlated with both temperature and soil moisture, suggesting that tropical rain forest oxisols are very sensitive to carbon loss with land use change.

What We Do Not Know About Carbon Storage and Flux in Tropical Forests

- Uncertainties in both the estimates of biomass and rates of deforestation contribute to a wide range of estimates of carbon emissions in the tropics. More studies are needed.
- Some studies show old growth ever-wet and semi-evergreen forests of Amazonia and Africa are increasing in biomass in response to elevated CO_2. Other studies (from Asia and Central America) suggest that this likely reflects a natural growth response to previous disturbance events. More long-term plot research is needed.
- In response to elevated CO_2, many models predict increased forest productivity, but recent studies suggest that stem growth rate actually decreased in the last 20 years largely due to increased nighttime temperature, decreased total precipitation, and increased cloudiness.
- Direct measurement of below-ground carbon stored in roots is often very difficult even with the most thorough root collection. Current estimates of root soil carbon in tropical forests could be underestimated by as much as 60%. Contrary to past assumptions, a significant portion of stored carbon exists below ground in tropical forests.
- Since many climate models predict further soil drying and increased litter fall in tropical forests, understanding the role of soil microbial communities in processes within the litter layer, belowground biomass, and soil carbon is key.
- Only three studies have analyzed land surface-atmosphere interactions in tropical forest ecosystems. It is essential to understand how carbon is taken up by plants and the pathways of carbon release, and how increasing temperatures could affect these processes and the balance between them.
- Better estimates are needed on the amount of mature, secondary, and disturbed forests in the tropics in order to better predict changes in carbon storage trends and the threat of release of this terrestrial sink.
- The effects of elevated atmospheric CO_2 and global climate change on herbivory and other plant/animal interactions in tropical forests are not well understood. Little research has been done in this area.
- Tropical dry deciduous and montane forests are almost a complete unknown because so little research has been done on these forest types. While the majority of dry deciduous forests in the Americas and Asia have been cleared, there is still a significant amount remaining in Africa and Mexico.

What We Think Are the Influences on Carbon Storage and Flux in Tropical Forests

- First and foremost, the primary risk to the carbon stored in tropical forests is deforestation, particularly converting forests to agriculture. Current estimates of carbon emissions from tropical deforestation vary greatly and are

difficult to compare due to differences in data sources, assumptions, and methods. Developing and incorporating multiple variables into new and existing ecosystem models for tropical forests is essential to determining carbon fluxes and future effects of deforestation and climate change.
- Combined climate-carbon cycle models predict that tropical forests are vulnerable to both short- and long-term droughts. The effects of drought will vary, depending on the forest type, whether or not the forest is water-limited, and the counter-effects of increased sunlight. At least in the short-term, tropical forests may be resilient to drought. However, this may be offset by increased vulnerability to fire after both short- and long-term droughts
- Changes in soil moisture affect not only the response of plant species and communities, but also the population dynamics of animals, fungi and microbes, which in turn will affect herbivory and decomposition. Elevated CO_2 reduces nitrogen-based defenses (e.g., alkaloids) and causes an increase in carbon-based defenses (e.g., tannins). As leaves exhibit lower nutritional value, herbivory may increase substantially to compensate.
- All large-scale wind and rain events are episodic and occur at relatively long time intervals that are difficult to predict. However, they drive the successional dynamics of forests, and therefore by implication, the above- and below-ground carbon stocks. Little to no work has been done on assessing and including this dynamism in the development of regional carbon models predicting future change. The assumption is that small-scale disturbances in old-growth forests will remain the dominant phase of growth.

How Might the Carbon Status of Tropical Forests Change with Changing Climate?

- The difference between the annual stand level growth (uptake: 2%) and mortality (release: 1.6%) of Amazonia is currently estimated to be 0.4%, which is just about enough carbon sequestered to compensate for the carbon emissions of deforestation in the region. This means that either a small decrease in growth or a small increase in mortality in mature forests could convert Amazonia from a sink to a source of carbon.
- It is difficult to model carbon flux and productivity in tropical forests due to their structural and age complexity and species composition. As a result, few ecosystem process models have been developed, parameterized, and applied within tropical forest systems. Nevertheless, it is a reasonable assumption that rising temperatures will increase the rate of most if not all biochemical processes in tropical plants and soils.
- In response to elevated CO_2, many models predict increased productivity, both in semi-evergreen forests of the Amazon and central Africa. However, on ever-wet sites in Panama and Malaysia, stem growth rate actually decreased from 1981 to 2005 largely due to increased nighttime temperature, decreased total precipitation, and increased cloudiness.
- Old-growth tropical forests are experiencing accelerated stand dynamics and increasing biomass. Most climate models and forest carbon balance models do not take forest composition into account. Forests with accelerated or "faster" dynamic have less biomass due in part to ecophysiological differences in plant growth.
- A warmer climate could drive low elevation forests to higher elevations or extend the range of tropical seasonal forests. However, if there is more deforestation in these seasonal and dry areas, there may be fewer species available that can migrate and adapt to warmer climates with drier soils.
- Many future climate scenarios predict soil drying in Amazonia and a general reduced capacity of the ecosystem to take up carbon. Understanding how tropical forests respond to water stress could be important because canopy-to-air vapor deficits and stomatal feedback effects could determine how tropical forest photosynthesis responds to future climate change.
- As tropical forest soils become drier, litter decomposition and its release of CO_2 from soil may slow in response to less water avail-

ability. However, there is also some evidence that methane release may increase as soils dry out.

- If drought becomes more common in tropical ever-wet and semi-evergreen forests, as some climate models predict, the likelihood of human-induced fires escaping and impacting large portions of the landscape increases.

1 Introduction

This chapter reviews current literature about carbon cycling in tropical forests. First the different types of tropical forests are described. This includes where they are found, their current and past extent, and their role in terrestrial carbon storage. Secondly we review how and where carbon is allocated in tropical forests, how carbon cycles, and how climate change may affect this cycling. Thirdly, we discuss how changes in carbon storage may occur through uptake, via photosynthesis, and through loss, via respiration and decomposition. The role of disturbance and its potential effects on stored carbon is also considered. Finally, the chapter concludes with a review of some of the threats to tropical forests and how they may influence climate change and elevated CO_2.

The level of interest in tropical forests has increased in recent decades due to global issues of climate change, biodiversity loss, and land use change (predominantly conversion of forest to agriculture). Globally, the tropical rain forest regions of Southeast Asia, South America, and Central Africa are some of the most rapidly developing areas of the world in terms of population growth, land conversion, and urbanization (Houghton 1991a; Soepadmo 1993; Nightingale et al. 2004). Tropical deforestation is one of the main contributing factors to the increase of CO_2 in the atmosphere (Houghton 1991a, b). Despite their importance and impact on the global carbon cycle, there is a lack of systematic assessment, and therefore knowledge, about the carbon pools and fluxes in tropical forests (Dixon et al. 1994; Lal and Kimble 2000; Nightingale et al. 2004). Although some generalizations can be made about tropical forest biomes across the globe, such highly diverse, complex systems warrant closer attention in order to make better estimates and predictions of global carbon budgets. Moreover, there is a tendency in carbon-related policy making to overlook the carbon cycle's interconnectedness with other biogeochemical cycles, such as water and nitrogen. None of these cycles occur in isolation; it is important to remember that carbon is related to biodiversity, water storage and filtration, and other ecosystem values.

Tropical forests occupy a broad range between the Tropic of Cancer and the Tropic of Capricorn, where moist air rising from the equatorial region loses this moisture in the form of precipitation as it descends over the tropics and subtropics (Heinsohn and Kabel 1999). These forests cover approximately 12% of the land surface and account for 50% of global forest area (Fig. 4.1). Approximately 8% of total atmospheric carbon dioxide cycles through these regions annually (Malhi et al. 1998). Tropical forests are responsible for nearly half of the total terrestrial gross primary productivity (Malhi et al. 1998). Consequently, they play a major, yet poorly understood, role in the cycling of carbon (Frangi and Lugo 1985; Soepadmo 1993; Foody et al. 1996; Malhi et al. 1998).

2 Tropical Forest Systems

Tropical forests can be divided into four broad types: (i) ever-wet (often called rainforest); (ii) semi-evergreen; (iii) dry deciduous; and (iv) montane (Fig. 4.1). Forests types have been categorized in relation to both the amount of precipitation and degree of seasonality as the main driver of productivity and decomposition, and hence carbon sequestration and loss.

2.1 Forest Type Descriptions

2.1.1 Ever-Wet Forests

Tropical ever-wet forests receive at least 100 mm of precipitation each month and at least 2,000 mm per year (Ricklefs 2001). Vegetation

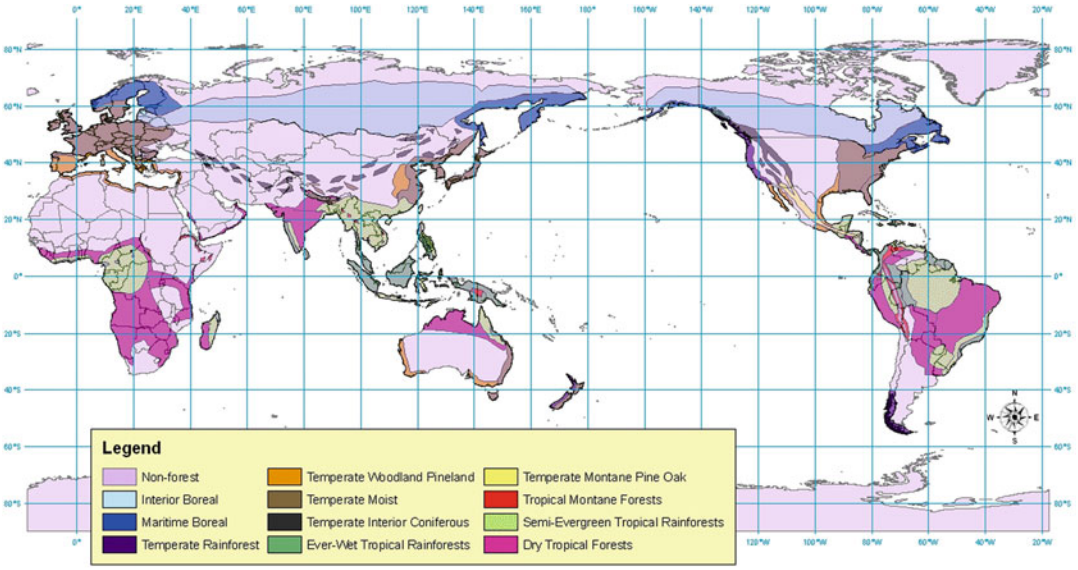

Fig. 4.1 Original extent of boreal, temperate, and tropical forest types of the world prior to land clearing

tends to be dense and of several strata (e.g., canopy emergents, canopy, lianas, epiphytes, treelets, shrubs, and herbs). The highly productive vegetation has adapted to this climate with the ability to immediately incorporate nutrients. As a result, many of the nutrients of tropical rain forest ecosystems are retained by the vegetation. Poorly planned and intensive logging or land clearance and burning can result in the loss of nutrients to the atmosphere and as run-off, thereby reducing the potential productivity of the landscape (Ricklefs 2001; Vandermeer and Perfecto 2005).

The majority of soils in ever-wet forests tend to be well-weathered ultisols, which are acidic, vary in fertility depending upon underlying geology, have relatively high cation exchange capacity, and are very susceptible to erosion. However, this is by no means consistent across the biome. Inceptisols predominate on young foothills, and andisols dominate on volcanic substrates. Both are characteristic of Central America and volcanic islands such as Sumatra, and both are fertile but strongly erodable (Fig. 4.2).

In West Africa, the ever-wet forest occurs along a thin strip of coast from Liberia to Ghana. It starts again in southeastern Nigeria, expanding across Cameroon and around the Gulf of Guinea. The wettest area of the region is the Cameroon Highlands, where rain fall at the base of Mt. Cameroon can reach over 12,000 mm per year. However, most of the area would be classified as marginally ever-wet, with rainfall in most of the range barely over 2,000 mm. Because of its ease of access for human populations, most of the coastal forest that historically spanned Cote d'Ivoire, Ghana, Nigeria, and Cameroon has been lost during the periods of French and British colonization with the commercialization of plantation crops such as coffee and cocoa (1930–1960), and now oil palm. Forests in these countries are now largely reduced to small, degraded patches.

The ever-wet rainforests were once expansive, covering all of eastern Central America (Atlantic Coast) from northern Costa Rica south through Panama, and along the Pacific coastal mountains of Columbia and northern Ecuador (Fig. 4.1). The other wet evergreen forest of the Americas covers the eastern foothills of the Andes and forms the upper basin of the Amazon. The wettest forests in Latin America are those straddling the Andes in the region known as the Chocó on the Pacific coast range of Colombia, and the

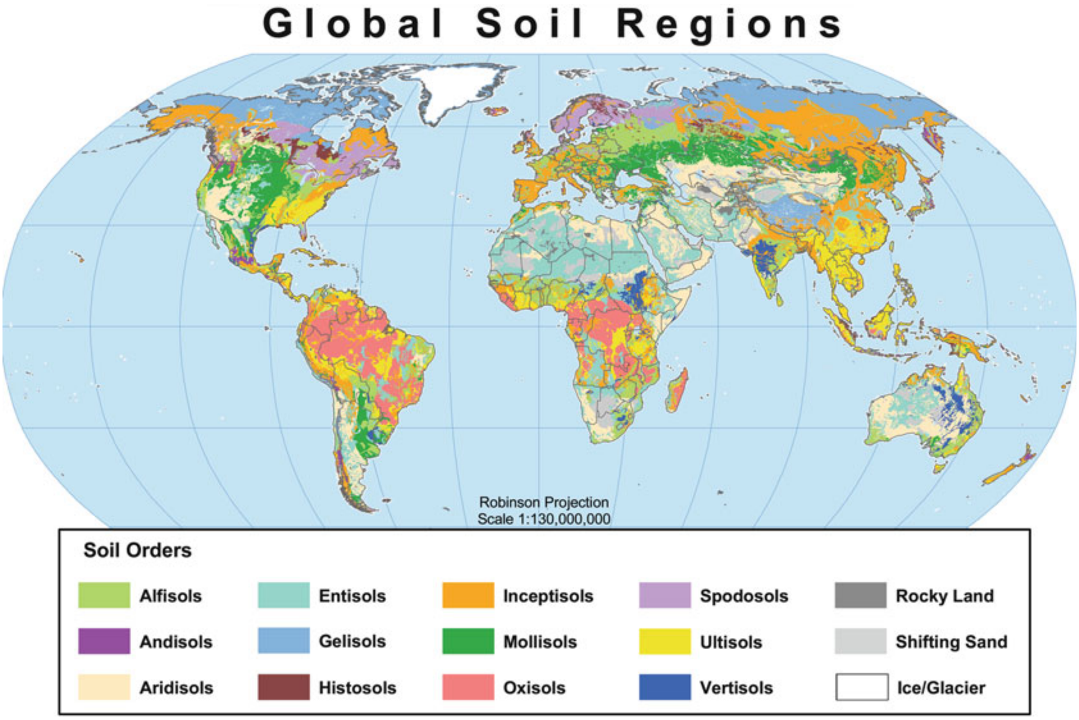

Fig. 4.2 A map depicting the major soil orders of the world (*Source*: From USDA 2005. Reprinted with permission)

upper Amazon of Ecuador. The Atlantic region of Central America has been difficult for people to access and still remains extensively forested, particularly in Panama and Nicaragua, as well as the upper Amazon regions bordering Colombia, Ecuador, and Peru.

The core Asian ever-wet forest can be considered the most moderated in seasonality largely because the land-sea margin and north–south mountain ranges serve as important sources of convectional and orographic precipitation during inter-monsoonal wet seasons. The heart of the ever-wet rain forest is in Borneo, Sumatra, New Guinea, and the Malay Peninsula, an area that makes up the largest extent of ever-wet rainforest in the world. Small areas also exist in southwest Sri Lanka, parts of the Western Ghats of India, and Mindanao in the Philippines.

Asia has had the longest legacy of rainforest commercialization (dating back 2,000 years), largely through maritime trade between Indian, Arab, and Chinese traders and the regional peoples. India's and Sri Lanka's forests are now largely restricted to the mountains and uplands of the countries, where historical land use for intensive rice cultivation, private tree garden systems, and plantation agriculture (tea, rubber, coconut – 1850–1950) has been happening much longer than elsewhere in Asia. Most of the ever-wet forest in the Philippines and Thailand is now confined to degraded patches, first logged over, and then subsequently and incrementally converted to village agricultural projects (1940–1985), many of which subsequently failed and are now wastelands. The Malay Peninsula had most of its lowland forest converted to plantation crops (rubber and oil palm) starting with the British (1900) but accelerating post independence (1948) such that most of the lowlands had been converted by 1980.

Substantial forest remains in the highlands but it is heavily cut over. A similar story exists for Sarawak and Sabah, the two east Malay states on Borneo. However, for these states, land conversion of the lowland forests occurred very rapidly and recently (1970–2000). Indonesia embarked on rapid logging and land conversion of its wet evergreen forests in Kalimantan (Indonesian Borneo) and Sumatra initially for colonization schemes (1970–1980), then more substantively as logging concessions. Subsequently, much of the logged over forest has been converted to oil palm plantations. In Borneo and Sumatra, both countries (Malaysia and Indonesia) have now embarked on clearing the remaining logged over forest for *Acacia mangium* pulp plantations or for oil palm (1995-ongoing). The remaining forested areas are restricted to the most unproductive soils and upland regions that are difficult to access. New Guinea (Papua and Irian Jaya, Indonesia) can be considered the last frontier of remaining large intact forest within the region, although much of it has been allocated for logging concessions (1990-ongoing).

2.1.2 Semi-Evergreen Forests

Tropical seasonally moist forests, also known as tropical semi-evergreen, like ever-wet forests, receive greater than 2,000 mm per year of rain. However, the forest type is more strongly seasonal (in Asia – monsoonal) with extended dry periods and then high periods of rain. Wet periods are generally longer than dry periods.

Soils are usually oxisols (or sometimes spodosols). They are both infertile soils, and acidic. Oxisols are highly weathered, with high clay content, and low cation exchange capacity (Clark et al. 1999; Vitousek and Sanford 1986). Oxisols dominate the uplands of the core Amazon and Congo basins. Alfisols, which are relatively more fertile, are usually found in seasonally drier climates that are not so strongly monsoonal. They predominate particularly in Indochina (India, Burma, Thailand, Cambodia, and Vietnam) (USDA 2002; Vitousek and Sanford 1986) (Fig. 4.2).

The greatest extent of semi-evergreen forest was that of the central and lower Amazon basin and the upper Orinoco of southern Venezuela. Much of the forest in the heart of the Amazon remains largely intact, but has been logged over through the use of the extensive river systems. Coastal and floodplain forests of the major rivers that flow into the Amazon have largely been converted to agriculture. The outer periphery of the basin (particularly on the southern side) and the coastal Atlantic forest of Brazil has retreated considerably because of colonization schemes and large land conversion to commercial soybean and ranching (1970-ongoing).

In West Africa, semi-evergreen forest dominates behind the band of coastal ever-wet rainforest, and can be considered a transition zone to dry deciduous forest further inland. Semi-evergreen forests also predominate in the central Congo River basin. The forests are generally more seasonal than those of the Amazon, with greater levels of deciduousness exhibited by some canopy species. Because of the difficulty of access, the inner core region of the Congo (Central African Republic, Republic of Congo, Democratic Republic of Congo, Gabon) largely remains whole, though current timber extraction is high (1990-ongoing). Both Amazon and Congo semi-evergreen forest can be considered by far the most important and largest tracts of tropical forest left in relation to forest carbon and climate change. However, Indonesia should be recognized for its significant peat forests that amount to the same amount of carbon emissions as the Amazon.

Indochina is the third region with semi-evergreen forest. The forest is found in parts of the Philippines, southern Thailand, northeast India/Burma, southeast Cambodia, southern Vietnam, northeast Sri Lanka, and the Western Ghats of India. The forest type is highly fragmented because of the physical geography and climate. This is an area of high soil fertility so most of the forest has been cut down and converted to agricultural use. The remaining forest patches are mostly degraded.

2.1.3 Tropical Dry Forests

Tropical dry deciduous forests can be defined as forests that shed their leaves during a dry season due to low water availability (Ricklefs 2001). They are located in the tropics and subtropics, mainly in Latin America, Africa, India, Australia and parts of Southeast Asia (Bullock et al. 1995). They can be located in rain shadows of mountainous regions and near mid-latitudes of convergence. Longer and more severe dry seasons support tropical dry seasonal forests and savannah ecosystems (Ricklefs 2001). Soils tend to be alfisols, entisols, and inceptisols (USDA 2002).

This gradient in moisture regimes across the biome has led to much debate over the extent of dry deciduous forests vs. savannahs in the drier tropics (Bullock et al. 1995). Dry deciduous forests are found on more fertile sites than savannas, although they can occur in the same climate zone. In many places, human intervention and fire govern the line between forest and savannah (Bullock et al. 1995). Tropical dry forests receive far less attention than tropical ever-wet and semi-evergreen forests, even though conservation concerns are high due to increased land use conversion, habitat fragmentation, and high levels of biodiversity and structural diversity (Bullock et al. 1995).

In Central America dry deciduous forest used to dominate the Pacific side of Nicaragua, El Salvador, Costa Rica, and Panama. Most of this forest has been cleared for ranching, but some is now coming back as secondary forest because ranching cannot be sustained, or along the coast because of land gentrification. Dry deciduous forest still dominates much of the Yucatan (Mexico, Guatemala) (Griscom and Ashton 2011). In South America, dry deciduous forests were extensive across the coast range and interior Pacific sides of the Andes in Colombia and Ecuador and in the Caribbean coastal mountains and interiors of the lower Orinoco. Most of this forest has now been converted to pasture, although in places second growth is coming back (Griscom and Ashton 2011). In the southern rim of the Amazon basin in Brazil, Bolivia, and northern Argentina, dry deciduous forests have been cleared for plantation agriculture and ranching. Little forest exists today except for some remnant patches in more remote areas.

Africa has the largest dry deciduous forest remaining, making up the miombo woodlands of Malawi, Zimbabwe, Tanzania, Angola, southern Democratic Republic of Congo, Mozambique and Botswana. It is an important resource for local people for firewood, timber, and grazing, and in some areas is heavily deforested. Nevertheless, the woodland in many areas remains relatively intact.

Dry deciduous forests also exist as small residual patches in what was extensive woodland in south India (east of the Ghats) across central India, Central Burma and Thailand, and interior Cambodia. Most forest is now converted to smallholder farms and degraded forest patches. Australia has considerable dry *Eucalyptus* woodland remaining across West and South Australia and in the north (Queensland and Northern Territories). However, a still greater portion has been cleared for raising sheep and for commercial agriculture.

2.1.4 Montane Tropical Forests

Montane tropical forest is the smallest in area (current and historical) compared to the other tropical forest types. Montane forest occurs above 3,000 m above sea level and is characterized by high precipitation (>2,000 mm per year) and lower amounts of radiation because of cloud cover. Epiphytes, particularly bromeliads, often characterize the groundstory and canopy. The greatest amount of forest of this type is in Latin America down the Cordierra of Central America and along the northern Andes from Venezuela to Peru. Asia has montane forests that are numerous but small, being largely confined to the tops of the Western Ghats (India), the central range of Sri Lanka, the highlands of Thailand, Cambodia, and Vietnam and the Ginteng Highlands of Peninsula Malaysia. Larger extents of montane forest exist as the backbone of the islands of Borneo and Sumatra, and the volcanoes of the Philippines. The greatest extent is on the plateaus and the jagged mountains of Papua New Guinea. Africa has only small amounts of montane forest on the slopes of the inland mountain systems of Central (Rwanda, Burundi) and East Africa (Kenya, Uganda and Tanzania).

The soils of montane forests are often some of the most productive and are mostly classified as inceptisols, which are high in soil organic matter (soil carbon), but are erosion-prone because of steep slopes. Many of the mountain regions adjacent to cities (Kuala Lumpur, Malaysia; Colombo, Sri Lanka; David, Panama; Quito, Ecuador; Bogota, Colombia; Nairobi, Kenya) have had their forests cleared for vegetable production, tea and coffee cultivation, and dairy. Much of the organic matter is lost through decomposition, and once depleted; such areas often revert to fire-prone invasive grass and fern lands.

3 Pools of Carbon in Tropical Forests

Tropical forests contain about 40% of the carbon in the terrestrial biosphere, an estimated 428 Gt of carbon, with vegetation accounting for 58%, soil 41%, and litter 1% (Soepadmo 1993; Watson et al. 2000). The carbon budget across tropical forest types can be further broken down into interrelated components: aboveground biomass, belowground biomass, litter, and soil carbon (Table 4.1). Aboveground biomass consists of live stems and large branches and often includes coarse woody debris (Malhi et al. 2004). Belowground biomass includes all root mass (Robinson 2007). Litter usually includes twigs, leaves, reproductive parts and other small biotic debris with short residence times (Malhi et al. 2004). What is included in soil carbon measurements, and how it is allocated within these categories, can vary from study to study. For example, some studies include the litter layer with the soil carbon analysis (e.g., Schwendenmann and Veldkamp 2005). Other researchers separate roots, large organic debris, and rocks from soil for analysis (e.g., Cleveland et al. 2007). No one method is superior. Each method comes with its own advantages and disadvantages depending on the research question. While the use of categories helps to facilitate measurement and analysis, it is also necessary to understand the level of flux between the various carbon pools. This is important not only to correctly measure each component of the carbon cycle, but also to determine the strengths of the links between pools and other biogeochemical cycles.

3.1 Aboveground Biomass

Aboveground biomass is generally derived from field inventory and forest cover data, extrapolated to forest biomass. Uncertainties in the estimates of both biomass and forest cover contribute to a wide range of estimates of carbon stocks in the tropics (Houghton 2005). Many analysts use the FAO estimates of aboveground biomass. These estimates are derived from national data provided by each country. Since countries often use different inventory systems and methods, comparisons between countries can be difficult. For example, the increase in biomass estimates in tropical forests of Latin America and tropical Africa seen in FAO data from the 1980s to the 2000s is most likely attributed to more forests being inventoried (Houghton 2005).

Biomass estimates also vary widely because different tropical forests allocate biomass in different ways in response to environmental conditions, and forest composition and structure. Some of variability, however, derives from factors related to how the data is collected, particularly data that are used to extrapolate from ground measurements to forest biomass. Another source of variability are the models that are used to predict biomass (eg those that do and do not use wood density as a proxy for carbon content). For example, measurements taken at the buttresses of individual trees and then extrapolated to total tree biomass have tended to inflate estimates of biomass in some past studies. (Malhi et al. 2004). Table 4.2 highlights some of the historical variability in above ground biomass estimates.

In response to elevated CO_2, many models predict increased productivity (Laurance et al. 2004; Lewis et al. 2004), both in semi-evergreen forests of the Amazon and central Africa. Feeley et al. (2007) found, however, that on seasonally wet sites in Panama and Malaysia, stem growth rate actually decreased from 1981 to 2005 largely due to increased nighttime temperature, decreased total precipitation, and increased cloudiness.

Decreases in stem growth rate may not be indicative of overall productivity decline, however. Trees could be shifting their allocation of resources from stem growth to root growth, leaf production and/or reproduction (LaDeau and Clark 2001). Nevertheless, even if overall productivity is increasing, decreased stem growth could affect carbon sequestration if, for example, the residence time of carbon in fine roots, leaves,

Table 4.1 A summary of carbon studies in tropical forests

	Site characteristics			Carbon pools				
Source	Location	Forest type	Age	Aboveground biomass	Coarse/fine woody debris stock	Coarse woody debris annual input	Belowground biomass	Soil
Malhi et al. (2004)	Lowland Amazon	Ever-wet/ semi-evergreen	Mature/old growth	Increment of 1.5–5.5 Mg C ha^{-1} a^{-1}				
Baker et al. (2007)	Upper Amazon/Peru	Ever-wet	Mature/old growth		24.4 ± 5.5 Mg C ha^{-1}	3.8 ± 0.2 Mg C ha^{-1} y^{-1} with a 4.7 ± 2.6 y^{-1} tunover		
Clark et al. (2001)	Costa Rica	Ever-wet	Mature/old growth	Increment of 1.7–11.8 Mg C ha y^{-1} (lower bounds); 3.1–21.7 Mg C ha^{-1} y^{-1} (upper bounds)				
Clark et al. (2002)	Costa Rica	Ever-wet	Mature/old growth		Fallen – 22.3 Mg C ha^{-1}; standing – 3.1 Mg C ha^{-1}	2.4 Mg C Ha^{-1} with a 9 y turnover		
Nepstad et al. (1994)	Lowland Amazon	Semi-evergreen	Mature/old growth					Between 1 and 8 m soil depth more soil carbon than above ground biomass; 15% soil carbon turnover
Feeley et al. (2007)	Lowland Malaya; Panama	Ever-wet	Mature/old growth	Decreases in growth recorded in 24–71% trees in Panama; 58–95% trees in Malaya				
Espeleta and Clark (2007)	Costa Rica	Ever-wet	Mature/old growth				Ten fold variation over 7 year period; four fold change across edaphic gradient of soil water availability/fertility	

Houghton et al. (2001)	Amazon	Ever-wet/ Semi-evergreen	Mature/old growth	Mean total standing and below ground biomass 177 Mg C ha^{-1}				
Lewis et al. (2004)	Amazon	Ever-wet/ Semi-evergreen	Mature/old growth	Basal area has been increasing at 0.10 ± 0.04 M2 ha^{-1} y^{-1} between 1971 and 2002				
Lewis et al. (2009)	Central Africa	Ever-wet/ Semi-evergreen	Mature/old growth	Above-ground biomass has been increasing at 0.63 Mg C ha^{-1} y^{-1}				
Phillips et al. (2008)	Amazon	Ever-wet/ Semi-evergreen	Mature/old growth	Above-ground biomass has been increasing at 0.62 Mg C ha^{-1} y^{-1}				
Robinson (2007)	Tropical Forests						68% higher amounts of below-ground biomass than previously estimated	
Paoli and Curran (2007)	Borneo	Ever-wet	Mature/old growth	Above-ground biomass increment 5.8–23.6 Mg ha^{-1} y^{-1}	Annual fine litter input 5.1–11.0 Mg ha^{-1} y^{-1}			Total amounts of annual NPP related to soil fertility – phosphorus
Whigham et al. (1991)	Yucatan, Mexico	Semi-evergreen	Early secondary		A hurricane can increase dead and downed coarse woody debris by 50%			
Wilcke et al. (2004)	Ecuador	Montane	Mature/old growth		9.1 Mg biomass ha^{-1}			

Table 4.2 Estimates of total biomass from various studies in tropical forests (mg dry weight per ha)

Above ground living biomass (mg dry weight)	Total above ground biomass (mg dry weight)	Below ground biomass (mg dry weight)	Reference
413.4	425.2	104.0	Russell (1983)
406.3		67.0	Klinge and Rodrigues (1973)
358.0	396.2		Delaney et al. (1997)
347.7	371.2	56.5	Grimm and Fassbender (1981)
346.0	395.0		Delaney et al. (1997)
343.0	351.0		Overman et al. (1994)
314.0	353.8		Delaney et al. (1997)
306.2	348.0		Uhl et al. (1988)
296.0	308.0		Delaney et al. (1997)
285.0	325.0		Brown et al. (1995)
267.0	320.0	68.0	Salomao et al. (1996)
264.0		35.4	Nepstad (1989)
221.0	247.3	58.2	Saldarriaga et al. (1988)
242.2	264.6	46.0	Fearnside et al. (1993)
140.0	155.2		Delaney et al. (1997)

Source: Modified from Houghton et al. (2001)

flowers, or fruits is shorter than in coarse woody material (Pregitzer et al. 1995).

Studies have found large differences in productivity between Southeast Asian tropical forests and those in the neotropics. In a meta analysis of 39 diverse neotropical forests (dry to wet, lowland to montane, nutrient-rich to nutrient-poor soils), total net primary productivity (NPP – above and below-ground) ranged from 1.7 to 11.8 Mg C/ha/year (lower bounds) and from 3.1 to 21.7 Mg C/ha/year (upper bounds) (Clark et al. 2001). In a tropical Asian ever-wet forest in southwest Borneo, however, Paoli and Curran (2007) found that above ground NPP alone ranged from 11.1 to 32.3 Mg C/ha/year, which implies that total NPP is much higher than in neotropical forests. Paoli and Curran (2007) also found that the spatial pattern of productivity in the lowland Bornean forests was significantly related to soil nutrients, particularly phosphorus. It is important to note that almost all the work cited here is from semi-evergreen and ever-wet forests of the Amazon, Central America, and Malaysia/Borneo. Little work has been done in other regions on this topic, especially in dry deciduous or montane forest types.

3.2 Belowground Biomass

Measuring belowground biomass is very difficult because roots are embedded in the soil. Not only is uncertainty in inventory data problematic for belowground biomass estimates, but direct measurement is often very difficult even with the most thorough root collection (Robinson 2007). Attempts to remove entire trees and their root systems tend to underestimate root biomass because many of the fine roots remain in the soil. Current estimates of root masses could be understated by as much as 60% according to Robinson (2007), who provides adjusted values for biomes to reflect this discrepancy. These findings suggest that root mass for tropical forests worldwide could contain up to 49 more Pg of carbon than found in previous studies, with a subsequent increase in total carbon sink of 9% for tropical forests (Robinson 2007). More belowground biomass could account for some of the "missing" global carbon sink and has implications for soil carbon estimates as well.

Understanding how belowground carbon allocation varies with soil and topographic conditions and across different climates is crucial to linking the different carbon pools in forests. Belowground biomass allocation can differ significantly both spatially and temporally in tropical forests. Spatial variation in belowground fine root biomass for an ever-wet forest at La Selva research station in Costa Rica was similar to that of studies done in other tropical and temperate forests (Espeleta and Clark 2007). Higher fine root biomass in the soil profile was associated with less fertile oxisols, lower in phosphorous, and with less soil water availability across a landscape gradient, while lower fine root biomass was associated with greater fertility and soil water availability in the soil profile. Espeleta and Clark (2007) produced the first belowground dataset for tropical forests to sufficiently assess temporal variation of fine root stocks. They found that sites on slope crests had greater live and dead fine-root variation in turnover due to changes in soil water content and its effect on nutrient acquisition. Drier years led to increased litter fall, and tree and root mortality. This has implications for how belowground biomass allocation and nutrient cycling may be impacted in a changing climate. If tropical forest soils dry as predicted by many models (e.g., Cox et al. 2000; Friedlingstein et al. 2006; Notaro et al. 2007), then fine roots located in the driest portions of the soil profile should die. If water stress does not lead to mortality, then plants should respond by allocating more root biomass to wetter areas of the soil profile.

3.3 Epiphytes, Litter and Logs

There have been numerous studies on the role of coarse woody debris in temperate forests, particularly old growth (Harmon et al. 1986). However few such studies have been done within tropical forests. Dry deciduous and semi-evergreen forests might have larger proportional loads of coarse woody debris than ever-wet and montane forests because of proneness to hurricanes and fire and greater impacts from swidden/fallow cultivation systems. For example, Eaton and Lawrence (2006) found that in the northern Yucatan, the largest amounts of downed debris were recorded post land clearance (88% of above ground biomass). Studies by others have shown that hurricanes can create large amounts of coarse debris, not directly, because most vegetation survives and re-sprouts, but indirectly through susceptibility to fire (Whigham et al. 1991).

Studies of coarse woody debris in ever-wet forests are also rare. One study in Costa Rica found no difference in standing dead and downed wood (>10 cm in diameter) in relation to topography and soil, but that overall dead biomass contributed to 33% of the above-ground biomass, with a turnover of about 9 years (Clark et al. 2002). In a semi-evergreen forest in the Brazilian Amazon, downed coarse woody debris was recorded between 50 and 55 Mg biomass per ha (Keller et al. 2004). For ever-wet forests in Costa Rica (Clark et al. 2002) and the Peruvian upper Amazon (Baker et al. 2007) stocks were about the same (22 and 24 Mg C per ha respectively or 46 and 50 Mg biomass per ha). In an Ecuadorian montane forest, Wilcke et al. (2004) found much lower woody debris biomass stocks (9 Mg biomass per ha) but it was highly variable and represented only 4% of the total estimated carbon in the forest.

Litter production in tropical forests is likely to increase in an elevated CO_2 environment as it is linked to higher respiration rates (Sayer et al. 2007). Litter production in the tropics, and indeed aboveground productivity, is related to soil nutrients, especially phosphorous, in addition to carbon (Paoli and Curran 2007). CO_2 enrichment tends to have a positive effect on plant growth up to a certain point before plants begin to exhaust other resources and reach a limit of enhanced growth, at which point litter production levels off.

3.4 Soil Carbon

Most soil carbon in tropical forests is located in the uppermost layers where root density is generally the highest. In a soil respiration measurement experiment comparing sites in Paragominas, Brazil (semi-evergreen) and La Selva, Costa Rica (ever-wet), Schwendenmann and Veldcamp (2005) found that more than 75% of the CO_2 was produced in the upper 0.5 m (including the litter layer) while less than 7% came from soil below 1 m depth. CO_2 production was positively correlated with both temperature and soil moisture in the top 0.5 m (Schwendenmann and Veldcamp 2005). In the Paragominas site, beyond 2 m in soil depth CO_2 production increased greatly with increasing temperature (Schwendenmann and Veldkamp 2005). Nevertheless, this is still a much lower amount of flux than in the upper layers. The increases in CO_2 production observed by Schwendenmann and Veldcamp (2005) indicate a strong positive feedback between ecosystem warming and CO_2 flux from moist tropical forest soils, but further studies need to verify this.

This study also highlights how differences in local climate, soil, and forest type can affect soil carbon flux. Paragominas is a tropical deciduous forest with a long dry season. Its forests have deep roots to a depth of at least 18 m (Nepstad et al. 1994) that enable trees to extract water stored at greater depths. Active soil water extraction occurs with root respiration, which can explain the high CO_2 production observed in the deep soil at the site in Paragominas (Schwendenmann and Veldkamp 2005). In contrast, the forest at La Selva does not experience an intense seasonal drought and the water content below 0.75 m is always above field capacity. The La Selva Forest also has a low root biomass below 2 m (Veldkamp et al. 2003). The contribution of root respiration to CO_2 produced beyond 2 m in depth at La Selva is minimal. Deep soil CO_2 at La Selva is principally from decomposition of soil organic carbon and/or dissolved organic carbon by soil microbes (Schwendenmann and Veldkamp 2005). The sheer contrast in CO_2 production at different depths of different soil and forest types highlights the complexity of soils and the need to further examine microbial and plant biochemical processes in deeper soil layers over longer periods (see Chap. 2 for further details).

The dynamic changes in the composition of the soil microbial community in response to inputs of organic matter may increase soil respiration rates and drive soil carbon losses in the form of carbon dioxide to the atmosphere (Cleveland and Townsend 2006; Cleveland et al. 2007). Since many climate models predict further soil drying and increased litter fall in tropical forests (e.g., Cox et al. 2000; Friedlingstein et al. 2006; Notaro et al. 2007), understanding the role of the soil microbial community and its function within the litter layer, belowground biomass and soil carbon is key. Changes in climate, the concentration of CO_2 in the atmosphere, and the nutrient content of litter could all have an effect on soil biota and decomposition rates (Coley 1998).

4 Biotic Drivers of Uptake and Release

Since the early 1980s, only three studies have analyzed land surface-atmosphere interactions in tropical forest ecosystems: the Anglo-Brazilian Climate Observation Study (ABRACOS; 1990–95); the Large-scale Biosphere/Atmosphere Experiment in Amazonia (LBA; 1996–2003); and the GEWEX Asian Monsoon Experiment (GAME; since 1996) (Nightingale et al. 2004). All three studies were conducted in semi-evergreen forests. It is difficult to model carbon flux and productivity in tropical forests due to their structural and age complexity and species composition. As a result, few ecosystem process models have been developed, parameterized, and applied within tropical forest systems (Nightingale et al. 2004). Nevertheless, it is a reasonable assumption that rising temperatures will increase the rate of most if not all biochemical process in tropical plants and soils (Lloyd and Farquhar 1996). Therefore, it is essential to understand how carbon is taken up by plants and the pathways of carbon release, and how increasing temperatures could affect these processes and the balance between them.

4.1 Photosynthesis and Autotrophic Respiration

Photosynthesis is the process through which plants assimilate carbon in the form of carbon dioxide (CO_2). Specifically, photosynthesis requires CO_2, sunlight, and water as inputs to produce glucose (carbohydrates), oxygen, and water. If the carbon uptake of photosynthesis exceeds the carbon efflux of respiration, intact forests are thought to remain a carbon sink (Phillips et al. 2008). However, the increases in productivity observed in Amazonian and Central African semi-evergreen and tropical forests over the past few decades by Phillips et al. (2008) and Lewis et al. (2009) cannot continue indefinitely. Lewis et al. (2009) estimate that one fifth of the CO_2 currently produced globally by land conversion and industrial emissions is absorbed by the tropical forest regions through increased productivity. However, if the increased atmospheric level of CO_2 is the cause for this increased productivity, then trees will eventually reach a saturation point and become limited by some other resource (Phillips et al. 2008). Thus, it is critical to consider the role of other biogeochemical cycles in relation to carbon.

Many future climate scenarios predict soil drying in Amazonia and a general reduced capacity of the ecosystem to take up carbon due to lack of water (Friedlingstein et al. 2006; Notaro et al. 2007). Understanding how tropical forests respond to water stress could be important because canopy-to-air vapor deficits and stomatal feedback effects could determine how tropical forest photosynthesis responds to future climate change (Lloyd and Farquhar 1996).

4.2 Heterotrophic Respiration and Decomposition

Respiration requires oxygen, carbohydrates, and water to release energy, CO_2 and water. Autotrophic respiration occurs when plants release CO_2 during biochemical processes, such as growth and production of chemical defenses. Heterotrophs (e.g., animals) also contribute to CO_2 release in a similar process. Like photosynthesis, respiration is linked to temperature fluctuations and other environmental factors (Phillips et al. 2008).

Decomposition is a type of respiration in which dead organic matter, oxygen, and water are transformed into CO_2, and water. Barring poor access to moisture and oxygen, decomposition in the humid tropics tends to be rapid, which limits the accumulation of detritus on the forest floor (Ricklefs 2001; Vandermeer and Perfecto 2005). Where moisture stress or oxygen stress inhibit aerobic respiration, however, detritus can accumulate, such as in peat swamps and other poorly drained areas or certain areas of tropical dry forests. When oxygen stress limits aerobic respiration, microbes and fungi responsible for decomposition rely on anaerobic respiration – a less efficient method of respiration in which methane is often a byproduct.

As tropical forest soils become drier, litter decomposition and its release of CO_2 from soil may slow in response to less water availability. However, Cattânio et al. (2002) found that greenhouse gas release in the form of methane, which has a higher global warming potential than CO_2, increased as soils dried in experimental water exclusion plots. This is surprising, as methane production requires anaerobic microsites that are uncommon in dry soils. Dry plots had more litter and woody debris; there was also anecdotal evidence of increased termite activity, which may explain the release of methane (Cattânio et al. 2002). Changes in soil moisture not only affect the response of plant species and communities, but also the population dynamics of animals, fungi and microbes, which in turn will have impacts on herbivory and decomposition. Thus, it is important to remember that changes in ecosystems rely on the interaction of all of its components, not just a few.

5 Disturbance: Abiotic Drivers of Uptake and Release

Disturbance is a natural process of all ecosystems, to which most organisms have some form of adaptation. Tropical forests experience tree mortality from old age, earthquakes or storms, which open up the forest floor to light and allow younger trees to attain the canopy. When trees die, they decompose and release CO_2 and nutrients to the soil and atmosphere. Nutrients may be taken up quickly by other plants, stored in soil for a period of time, or leached from the system during rain events. In large scale disturbances, especially fires, landslides, land clearance, or logging, large amounts of nutrients are lost from the ecosystem. It may take hundreds of years to recover from this nutrient loss. At the same time, land-use conversion to non-forest uses, such as farming and urban development, releases carbon to the atmosphere, further altering the carbon budget of the landscape.

Many studies use old growth forests that have not experienced major disturbances for a long period of time (e.g., Malhi and Phillips 2004). This has led to unexpected results in carbon flux measurements. In one 3-year study of old growth forests in the Amazon, carbon was released in the wet season and taken up in the dry season, in opposition to the seasonal cycles of both tree growth and model predictions (Saleska et al. 2003). This disconnect was attributed to decomposition and soil moisture availability, and transient effects of recent disturbance. This has important implications for carbon budgeting in the Amazon. If studies tend to be concentrated in undisturbed, old growth forests versus recently or regularly disturbed sites, predictions of future carbon sequestration rates are likely to be overestimated (Saleska et al. 2003).

5.1 Drought and El Niño-Southern Oscillation (ENSO) Events

ENSO events and droughts are part of the planet's natural climate cycles. Although there has been much research into ENSO events and their effect on droughts in the tropics, droughts can be independent of ENSO events. Combined climate-carbon cycle models predict that the Amazon forests are vulnerable to both short- and long-term droughts (Samanta et al. 2010). When water is initially limited, vegetation responds by reducing transpiration and photosynthesis, which in turn reduces the amount of water recycled to the atmosphere.At least in the short-term, some tropical forests may be resilient to drought through deep roots. However, this may be offset by increased vulnerability to fire after both short- and long-term droughts (Saleska et al. 2007; Nepstad et al. 2007).

Tropical rainforests in the Amazon and southeastern Asia typically suffer from droughts during ENSO events. These droughts are more severe during strong El Niño years (Lyons 2004). Ever-wet forests and semi-evergreen forests response to drought varies. In one study of the ever-wet forests of Borneo, where droughts are rare, mortality increased during strong El Niño years due to severe drought, while semi evergreen forests experienced relatively little change (Potts 2003). In addition to forest type, position in the landscape, soil texture and rooting depth play a role in the vegetation's response to drought (Sotta et al. 2007). For example, temporarily flooded valleys and lowlands often receive drainage from upslope areas and are able to retain moisture longer than uplands (Ashton 1992; Ashton et al. 1995; Grogan et al. 2003; Ediriweera et al. 2008). Areas with finer soil textures retain more water for longer time periods than those with coarser textures. Texture can vary within the soil profile, which means that the texture of soil at lower depths could be an important indicator for a site's water retention capacity during droughts (Grogan et al. 2003; Sotta et al. 2007). In addition, the location of roots within the soil profile determines where a plant can take up water. During drought events, the surface tends to dry first, giving plants with deeper roots or the ability to quickly respond to drought by allocating root growth to deeper soils an advantage (Sotta et al. 2007). Increased water stress during drought is linked to higher tree and liana mortality, which suggests that more carbon will be released through decay and increased probability of fire (Nepstad et al. 2007). These differing responses are significant because ENSO events are expected to become more frequent in response to climate change (Tsonis et al. 2005).

5.2 Wind and Rain

Wind throw and snap-off of trees from winds can occur in a variety of forms from large landscape level effects (hurricanes and typhoons) to more landscape-specific convectional windstorms that affect multiple trees (stand scale) to individual wind throw and branch breakage (Whigham et al. 1999). Most winds come with rain, either before or after these events. Rain-soaked soils are less firm, and roots insecure, making trees more prone to windthrow.

Seasonality provides another axis for differentiation. Subtropical forests and regions more than 10° north or south of the equator experience greater variation in climate, and therefore stronger trade winds, monsoons (and hurricanes), particularly on the eastern sides of continents (e.g. Honduras, Belize, Yucatan-Mexico, Guatemala, Nicaragua, southeastern Africa, Madagascar, Vietnam, eastern coast of the Philippines, southeast China, the Caribbean islands, the southwest Pacific Islands, northeast Australia) (Whigham et al. 1999). These regions can be exposed to periodic large scale wind events which leads to rapid regrowth following such events, due to the large quantity of tree species that vigorously resprout (Whitmore 1989; Brokaw and Walker 1991; Whigham et al. 1991; Vandermeer 1996; Vandermeer et al. 1997, 1998; Eaton and Lawrence 2006). Most forests in these regions would be considered semi-evergreen or dry deciduous – meaning that periods of drying can promote fire (often human caused) for land clearance. In fact, many swidden systems are cleared during the dry season and then burned prior to the rains to take advantage of the pulse of nutrients for crop cultivation in the wet season.

In the more equatorial regions where ever-wet forest dominates, winds often occur with the onset of rains through vigorous frontal or convectional thunderstorms that can knock over large swaths of forest with strong down drafts (Whigham et al. 1999). On steeper and often younger more erosion-prone hills and mountains, large amounts of rain can cause landslides, riparian flooding and bank erosion (e.g. in the Andes, Central American Cordierra, central ranges of Sumatra, Borneo, and Malay Peninsula). All large scale wind and rain events are episodic and occur at relatively long time intervals that are difficult to predict. However, they drive the successional dynamic of forests, and therefore by implication, the above- and below-ground carbon stocks. Little to no work has been done on assessing and including this dynamism in the development of regional carbon models predicting future change superimposed upon which, is young second-growth forest, originating after agricultural cessation.

5.3 Fire

Fires in tropical forests are typically the result of drought and human land management practices (Bush et al. 2008). Indeed, fire is thought to be a more imminent threat to tropical forests than climate change (Barlow and Peres 2004; Nepstad et al. 2004; Bush et al. 2008). In contrast to other biomes, such as certain jack pine (*Pinus banksiana*) boreal forests where fire events tend to be naturally occurring, humans have been the primary ignition source of fires in tropical forests since pre-Columbian times. In fact, natural fire in the Amazon has been so rare since the mid-Holocene that the presence of charcoal in soil is an indicator of human activity (Bush et al. 2008). Under normal moisture conditions, the likelihood of fire decreases exponentially with distance from roads and clearings (Cochrane and Laurance 2002). This supports the view that fire is a direct result of human activity in tropical systems. If drought becomes more common in tropical forests as some climate models predict (e.g., Cox et al. 2000), the likelihood of human- induced fires escaping and impacting large portions of the landscape increases. This was seen during the ENSO-induced drought in tropical Indonesia and Amazonia in 1997–1998 where drought caused many human-ignited fires to escape and become wildfires (Bush et al. 2008).

In addition to climate, the impact of fire on tropical forests is also highly linked to forest structure. Nepstad et al. (2007) found that mortality of large trees and lianas following an experimental drought increased. Large trees not only store significant amounts of carbon, but also provide shade, which helps to keep litter moist. The absence of this shade dries out the litter layer and the dead lianas become ladder fuels, thus increasing the probability that an escaped fire will burn the litter layer and reach the canopy (Nepstad et al. 2007). This in turn is likely to impact what types of plants can regenerate and colonize after a fire.

5.4 Herbivory

The effects of elevated atmospheric CO_2 and global climate change on herbivory and other plant/animal interactions in tropical forests are not well understood. Little research has been done in this area. One seminal piece, Coley's "Possible effects of climate change on plant/herbivore interactions in moist tropical forests" (1998) addressed the interdependent roles of climate change and herbivory in tropical forests. More research into how climate change and elevated greenhouse gases will affect herbivore-plant and other predator–prey dynamics is needed. Indeed, although the Coley study is a core research paper on this topic, even this study is not adequately supported by direct experimentation.

6 Climate Change Impacts on Tropical Forest Dynamics

6.1 Increased Productivity Versus Increased Respiration

Many old-growth tropical forests are showing increases in biomass (Malhi and Phillips 2004; Lewis et al. 2009). Studies have shown that there has been a net increase in biomass in recent decades in several Amazonian and Central African semi-evergreen and ever-wet forests. Several studies have addressed methodological challenges in measuring biomass (Baker et al. 2004; Chave et al. 2004). According to new estimations by Malhi and Phillips (2004), the net carbon sink of intact old growth forests of Amazonia is 0.9 ± 0.2 Mg C per ha per year. Applying this rate to the area of moist forest in Amazonia, the Amazon rain forest is thought to sequester nearly 0.6 Pg C per year (Baker et al. 2004).

Like many ecological processes, biomass growth does not occur in isolation. Forest turnover rates in Amazonia have accelerated (Phillips et al. 2004; Laurance et al. 2004). In particular, the greatest increases in turnover rates have occurred on more fertile soils in western Amazonia. This increase in recruitment has been greater than the increase in mortality, which has actually lagged behind this acceleration in growth (Phillips et al. 2004). Similarly, Laurance et al. (2004) found that forests of central Amazonia have experienced changes in dynamics and composition that are not due to any detectable disturbance. In a network of 18 permanent study plots, not only have mortality, recruitment, and growth rates increased over time, but 27 of 115 relatively abundant tree genera have changed significantly in population density or basal area.

However, in a study based on large-scale plots in other tropical regions (mostly Asia, Central America) results do not support the hypothesis that fast-growing species are consistently increasing in dominance in tropical tree communities (Chave et al. 2004). Instead, results suggest that the forests are simultaneously recovering from past disturbances and affected by changes in resource availability. More long-termstudies are necessary to clarify the contribution of global change to the functioning of tropical forests (Chave et al. 2004). What is certain, however, is that these changes in dynamics and composition could have important impacts on the carbon storage and biota of Amazonian forests (Laurance et al. 2004).

In addition, as mentioned previously, most climate models and forest carbon balance models do not take forest composition into account (Phillips et al. 2008). Forests with accelerated or "faster" dynamic have less biomass due in part to ecophysiological differences in plant growth. For example, fast growing species have less dense wood, and therefore less stored carbon, compared to slow-growing species which have denser wood, with more carbon. Early successional forest therefore has less carbon stored than late sucessional forest (Phillips et al. 2008). A summary of how increasing CO_2 concentrations may or may not affect tropical forest growth is provided in Table 4.3 (Malhi and Phillips 2004).

Table 4.3 Arguments to expect, or not, substantial effects of increasing CO_2 concentrations on tropical forest growth and carbon balance (direct and indirect effects are considered, including climate change)

Zero or negative effect on growth and carbon storage	Positive effect on growth and carbon storage
Leaf level	
Increased respiration and photorespiration caused by rising temperatures	Direct fertilization of photosynthesis by high CO_2
Warming temperatures lead to increased evaporative demand, inducing stomatal closure and reducing photosynthesis	Reduced photorespiration caused by high CO_2
Increased emissions of volatile hydrocarbons at higher temperatures consume assimilated carbon	Improved water-use efficiency caused by high CO_2
	Photosynthetic rates increase with moderate warming optimum temperature for photosynthesis rises with rising CO_2
Plant level	
Plants are often saturated with respect to non-structural carbohydrates?	Excess carbon may be used preferentially above ground to acquire rate-limiting resource (light) by investing in wood
Plant growth limited by nutrients other than carbon (N, P, K, Ca)	Excess carbon may be used preferentially below ground to acquire rate-limiting resource (nutrients) through fine root development or supporting P-scavenging mycosymbionts
Rising soil temperatures increase soil acidification and mobilize aluminium, reducing soil nutrient supply	Rising temperatures increase soil mineralization rates and improve nutrient supply
Plant carbon balance is limited by respiration costs rather than by photosynthesis gains?	
Acclimation (downregulation of photosynthesis) limits any response to increasing CO_2	
Stand level	
Biomass ultimately limited by disturbance (e.g. windthrow risk) rather than by resources	Faster growth leads to some biomass gains, with mortality gains lagging
Forest canopies are close to physical limits of forest structure which cannot be increased (e.g. maximum tree height is limited by hydraulics or mechanics)	Rising CO_2 improves water-use efficiency and reduces tension in the water column, allowing an increase in maximum tree height for a given cross-sectional area
Faster growth and turnover may favour disturbance-adapted taxa, with less dense wood	Faster growth and turnover may prevent stand dominance by senescent ‘over-mature’ trees with high respiration costs, creating positive feedback on stand-level growth rates
Lianas may benefit from increased CO_2 and disturbance, limiting biomass gains by trees	Improved forest water balance leads to reduced drought mortality and fire incidence
Mortality rates increase because of climatic warming and/or drying, or increased climatic variability	
Climatic drying combined with forest fragmentation and degradation lead to increased fire frequency	

Source: From Malhi and Phillips (2004). Reprinted with permission

Tropical forests are resilient to many types of environmental change. However, given the human footprint in many of these forests, the expected resiliency may not materialize (Cowling and Shin 2006). Evergreen rain forests have dominated the Amazon Basin since the last glacial maximum (Beerling and Mayle 2006). Historically, climate change has driven biome shifts in transition or ecotonal zones, while CO_2 changes have led to increased carbon storage (Beerling and Mayle 2006). Many transition zones (e.g., montane forests) and tropical seasonal forests are areas that have experienced rampant deforestation and other types of land-use change in the past century. This may yield some insight into how tropical forests might change in both composition and range in response to climate change (Malhi and Phillips 2004). For example, a warmer climate could drive low elevation forests to higher elevations or extend the range of tropical seasonal forests. However, if there is more deforestation in these seasonal and dry areas, there may be fewer species available that can migrate and adapt to warmer climates with drier soils (Malhi and Phillips 2004).

Many models have predicted decreased forest cover and soil drying over Amazonia in response to the radiative effect of rising CO_2 concentrations in the atmosphere (Friedlingstein et al. 2006; Notaro et al. 2007). What happens to soil carbon pools and the dead biomass from this reduced forest cover is of great importance to researchers studying carbon fluxes under climate change. The fate of these carbon pools under the most extreme scenario modeled – wide-spread tree die-off – depends on drought conditions and elevated soil respiration under higher temperatures (Cox et al. 2000). As air temperature rises, respiration increases, while carbon uptake from photosynthesis continues until it reaches some threshold. In short, the current carbon sink that intact tropical forests provide cannot continue in the same manner indefinitely. How this carbon balance could change, apart from the immediate threats of land use change, habitat fragmentation and fire, is uncertain.

Phillips et al. (2008) provide three scenarios about the future of this carbon sink in the Amazon based on an extensive network of research sites: mature Amazonian forests will either (i) continue to be a carbon sink for decades (Cramer et al. 2001); (ii) quickly become neutral (i.e., uptake equals release) or a small carbon source (Cramer et al. 2001; Körner 2004; Laurance et al. 2004) or (iii) become a mega-carbon source (Cox et al. 2000; Lewis et al. 2006). The difference between the annual stand level growth (uptake: 2%) and mortality (release: 1.6%) of Amazonia is currently estimated to be 0.4%, which is just about enough carbon sequestered to compensate for the carbon emissions of deforestation in the region (Phillips et al. 2008). This means that either a small decrease in growth or a small increase in mortality in mature forests could convert Amazonia from a sink to a source of carbon (Phillips et al. 2008). Better estimates are needed of the amount of mature, secondary and disturbed forests in the Amazon in order to better predict changes in carbon storage trends and the threat of release of this terrestrial sink.

6.2 Changes in Precipitation Amounts and Patterns

Some models have predicted that reduced forest cover and soil drying over Amazonia, in response to the radiative effect of rising CO_2 concentrations in the atmosphere, will result in a reduction in the land's capacity to take up carbon (Friedlingstein et al. 2006; Notaro et al. 2007). In simulation modeling of ecosystem threshold responses to changes in temperature, precipitation, and CO_2, Cowling and Shin (2006) found the 'natural,' intact Amazonian rainforest to be resilient to environmental change, particularly to decreases in temperature and precipitation. However, they also warn that humans have changed these forests so quickly in the past several decades that the resiliency of the Amazonian rain forest is at risk (Cowling and Shin 2006). Asian ever-wet forests are thought to be considerably more sensitive to drying conditions (Paoli and Curran 2007). However, the interactions with other human disturbance factors such as land clearance, edge effects and fragmentation, and fire need to be considered and could have important negative feedback influences (Leighton and Wirawan 1986).

6.3 Land Use Change

Human intervention through deforestation and forest degradation has been the leading cause of perturbation to the carbon cycle in tropical forests (Houghton 1991a; Sampson et al. 1993). As a result, by the year 2050, the tropics could be a source of atmospheric CO_2 (Sampson et al. 1993). Land use change is perhaps the most imminent threat to the ecosystem services that tropical forests provide. It is believed that land use change could lead to the release of 40–80 Pg C per year over the next 50 years (Nightingale et al. 2004).

6.3.1 Deforestation

Deforestation affects the carbon balance of tropical forests and climate feedback cycles in two principal ways: carbon emissions from deforestation and the albedo effect of deforested lands (Bala et al. 2007; Ramankutty et al. 2007). Moreover, for every ton of carbon released to the atmosphere through deforestation, 0.6 additional tons of carbon are released through degradation of the remaining forest (Houghton 1991a). However, current estimates of carbon emissions from tropical deforestation vary greatly and are difficult to compare due to differences in data sources, assumptions, and methods (Ramankutty et al. 2007). Developing and incorporating multiple variables into new and existing ecosystem models for tropical forests is essential to determining carbon fluxes and future effects of deforestation and climate change (Nightingale et al. 2004). In order to fully quantify the carbon emissions from tropical deforestation, one must account for initial carbon stock of vegetation and soils, influence of historical land use, rates and dynamics of land-cover changes, methods of land clearing and the fate of the carbon from cleared vegetation, response of soils following land-cover change, and the representation of processes in ecosystem and climate models used to integrate all of these components (Ramankutty et al. 2007).

While it is a fact that deforestation releases CO_2 to the atmosphere, which in turn has a warming effect on climate, there is another important piece of the deforestation equation that some models neglect. Deforestation comes with biophysical effects on climate, such as changes in land surface albedo, evapotranspiration, and cloud cover. Simulations out to 2150 by Bala et al. (2007), using a three-dimensional model representing physical and biogeochemical interactions between land, atmosphere, and ocean, found that at a global level, deforestation has a net cooling effect on climate. This is because the net cooling influence of changes in albedo and evapotranspiration outweigh the warming effects associated with carbon release (Bala et al. 2007). It is noteworthy that the model predicted different effects associated with the deforestation of tropical vs. temperate and boreal forests. According to the model results, afforestation in the tropics would be beneficial because of the greater role of tropical forests in increasing evapotranspiration, CO_2 sequestration, and cloud cover and thus reducing the heating impacts of global warming. In contrast, deforestation of higher latitude boreal forests would greatly increase albedo relative to evapotranspiration and CO_2 sequestration having an overall positive effect on climate (Bala et al. 2007). It must be emphasized that this is a single study involving simulations so caution needs to be used in interpreting these results.

6.3.2 Agriculture

Expanding crop and pasture lands have a profound effect on the global carbon cycle as tropical forests typically store 20–100 times more carbon per unit area than the agriculture that replaces them (Houghton 1991a). In the Amazon, the growing profitability of large-scale industrial agriculture and cattle ranching has led to significant deforestation. This will only increase forest fragmentation and degradation and subsequent climate effects as it continues to expand (Nepstad et al. 2008). The use of fire to clear forested lands may exacerbate changes to carbon cycling since fire fills the atmosphere with aerosols, thereby reducing transpiration (IPCC 2007).

Within Southeast Asia, the conversion of tropical forests to oil palm plantations is accelerating. This land use change results in a significant net loss of carbon to the atmosphere since the aboveground biomass of oil palm plantations stores less carbon (<36–48 tons C/ha) than tropical primary forests (235 tons C/ha) (Reijinders and Huijbregts 2008). Including carbon releases for fire, which is the primary method for land clearing, the net carbon loss from the system may be as much as 187–199 tons C/ha. If such fires are of high intensity, there is even greater loss of soil carbon (Reijinders and Huijbregts 2008). A full life cycle analysis of forest conversion and carbon loss, and then cultivation and production of biofuels from oil palm, puts into question the assertion that oil palm reduces CO_2 emissions (Reijinders and Huijbregts 2008).

7 Conclusion and Summary Recommendations

Tropical forests account for almost half the gross primary productivity of the world's terrestrial ecosystems.

- Tropical ever-wet and semi-evergreen forests in the Amazon and southeastern Asia typically suffer from droughts during ENSO events. In the short term, tropical forests may be resilient to drought, but increased susceptibility to anthropogenic fire may negate this.
- In tropical ever-wet forests, where droughts are rare, mortality may dramatically increase. Seasonal semi-evergreen forests may show little change.

In tropical forest regions humans have caused most fires. If climate model predictions are correct, increased drought will promote the escape of human-caused fires that will impact large portions of the remaining forest.

- More work should be done to investigate the negative and positive feedbacks of drought, windstorms, insects/pathogens, fire and humans, and their interactions, on the forest dynamic – and in particular, their effects on carbon.

According to long-term permanent plot data, old growth ever-wet and semi-evergreen forests show increasing biomass in recent decades in Amazonian and Central African forests. In contrast to climate model predictions, this increase in forest biomass may reflect forest response to previous natural and anthropogenic disturbances (Chave et al. 2004).

Uncertainties in estimates of both biomass and deforestation contribute to a wide range of estimates of carbon emissions in the tropics.

- Better estimates are needed of the amount of mature, secondary, and disturbed forest in order to better predict changes in carbon storage trends.
- Dry deciduous and montane forests are almost a complete unknown because so little work has been done on these forest types; therefore, much more research needs to be carried out in these areas.
- Even though in the Americas and Asia many dry deciduous forests have been cleared, significant amounts remain in Africa.

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