Chapter 17 Tropical Rain Forests as Old-Growth Forests

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17.1 Introduction

In the context of this book, we may begin by making the general observation that many rain forests are *par excellence* old growth forests. They have the diagnostic characteristics mentioned in the companion chapter (Chap. 2 by Wirth et al., this volume), including mixed ages and species, and large amounts of standing and downed deadwood in all stages of decay. Some authors use the term 'virgin' to describe them, but generally they are not at all virgin, having been colonised by indigenous people in former times using slash and burn agriculture and undergone re-growth for several hundreds of years (Clark 1996). This is known from artefacts and charcoal found in the soil (Gomez-Pompa et al. 1987). We also recognise 'old growth secondary forest', which may have remarkably high biomass and much of the general appearance of undisturbed forest but lacks some of the biodiversity and the old and dead trees (Brown and Lugo 1990).

The status of tropical rain forests is widely discussed in the literature. These forests occupy some 12% of the terrestrial surface; they contain 55% of the biomass; they are thought to hold over half of the global biodiversity. They occupy the warm and wet regions of the Earth, occurring where the temperature of the coldest month is at least 18°C, and where every month has 100 mm of rain or more. One can argue to some extent with these figures, as the definition of tropical rain forest is not hard and fast (see for example, Richards 1952; Clark 1996; Whitmore 1998). We may adopt one of the first definitions (Schimper 1898):

Evergreen, hygrophilous in character, at least 30 m tall and usually much more, rich in thick-stemmed lianas and in woody as well as herbaceous epiphytes.

Tropical rain forests are disappearing at a rate that is also generally disputed, but which is somewhere between 0.4 and 0.6% per year, corresponding to 4–6 millions of hectares per year (Achard et al. 2002; and Chap. 18 by Achard et al., this volume). Political awareness of their real value as a resource and as a global environmental service is now higher than ever before, and there are signs that steps may be taken to reduce deforestation rates (see Chap. 20 by Freibauer, this

volume), although this requires international initiatives, which will take some time. We will return to this aspect later.

The aim of this chapter is to comment on the structure and function of the rain forest canopy, inasmuch as it influences, and generally interacts with, the global climate.

17.2 Structure

Numerous authors have commented on the vertical stratification of rain forest canopies, asserting that a distinguishing feature of rain forests is that the canopy forms strata or storeys. The earliest author to put forward this point of view may have been von Humbolt (1808); later the concept was championed in the Englishspeaking world by Richards (1952), whilst elsewhere there was a focus on the diversity of individual tree architecture (Hallé et al. 1978). The evidence for stratification comes from profile-drawings, in which a high degree of subjectivity may have influenced the result. When attempts have been made to describe the distribution of leaf area in an objective way, either by felling trees and cutting them into segments corresponding to different heights (Kira 1978, McWilliam et al. 1993), by photographic survey inside the canopy using suspension-wires (Koike and Syahbuddin 1993) or from a tower with photography (Meir et al. 2000) or stateof-the-art canopy sensors (Dominguez et al. 2005), the canopy does not show the discontinuities that one might expect from the stratification paradigm (Fig. 17.1). In fact, it is similar to that found in other forests, differing only in scale: the rain forest is taller than most temperate forests and the canopies of the tallest trees are broader. There is, however, vertical stratification in another sense. Recognisably different life forms are present at different heights, and they occupy different levels within the continuum. The tall-growing emergent species are sparse and often have the discoid individual canopies that give rain forest its characteristic appearance; underneath these is the main canopy made up of trees with lianas and epiphytes [Richards (1952) recognised two of these layers], beneath that we have a conspicuous understorey or ground layer of palms, seedlings, saplings and herbs. The light climate at ground level is complex, but this applies equally to all old-growth forests (Montgomery and Chazdon 2001; see also Chap. 6 by Messier et al., this volume). In all of these, the radiation is different from normal daylight in the following: spectral distribution, planes of polarisation, directional distribution, temporal patterns and, most importantly, it has a much diminished flux density, typically only a few percent of daylight.

Several claims are commonly made of rain forest canopies from a theoretical point of view. One is that the discoid emergent trees create a special light climate, with sun-flecks at a different angular elevation to that of temperate forests (Terborgh 1985); another is that tropical forests can support twice the leaf area of temperate forests (Leigh 1975). After several decades of research, neither of these assertions have much observational support. Leaf area index (LAI) has usually been measured indirectly by optical means, and this introduces uncertainty into its determination



because leaves are clumped together instead of being random and, moreover, optical methods do not usually distinguish leaves from stems and branches. Where it has been measured destructively (Kira 1978; McWilliam et al. 1993), the LAI is in the range 5.0–7.5. It is clear that deciduous forests in the temperate parts of the world also have leaf area indices in this range, although they can often be lower, and certainly do become lower in old-growth as a result of trees falling (Eriksson et al. 2005). Another misrepresentation of rain forests is that they hold extremely large and very old trees; in fact the trees are not usually extremely old, although a few of them are indeed very large. Chambers et al. (1998) made determinations of age of emergent trees using ¹⁴C measurements in rain forest at Manaus, Brazil, and discovered a few slow-growing trees over 1,000 years old; however, most were fast-growing and younger (Fig. 17.2).

How then is the structure of the rain forest canopy really different from the temperate deciduous canopy? Here we identify two aspects. The first is that the canopies of individual trees are often tied together with lianas. This means that when one large tree is blown down, other trees are damaged and sometimes uprooted too, leading to a more complex disturbance regime, and a larger scale of spatial variation than in other canopies, which probably has led to a rather different selection pressure on seedlings. Earlier authors commented on the regeneration niche of rain forests, and the way that tree species may have become specialists for



Fig. 17.2 The average long-term growth rates in diameter of large emergent trees from a forest near Manaus, Brazil. Growth rates were obtained by dividing the diameter of the stem by the age of the tree. The age was determined by radiocarbon dating. Data from Chambers et al. (1998)

particular types of gaps (Denslow 1980), although ecophysiological investigations do not generally support such a high degree of categorisation as has sometimes been claimed (Brown and Whitmore 1992). The second aspect is that the vertical pattern of LAI is large, i.e. the leaf area is spread over a height of up to 50-60 m. One aspect of this is that there are large volumes of air in between leaves and branches. This has implications not only for microclimate but also for habitats, especially of flying animals. It also has some interesting implications for storage of heat and gases that mean that the lower part of the canopy is relatively decoupled from the atmosphere and may become considerably rich in carbon dioxide and other gases that emanate from the soil. It may be the diversity of microclimates resulting from the immense structural heterogeneity that contributes to the great richness of non-tree plant species, epiphytes in particular (Gentry and Dodson 1987). An example of microclimate from the present authors' work relates to CO_2 . In the rain forest canopy, CO₂ builds up to high concentration at nights when the external conditions are stably stratified (Fig. 17.3). This is the outcome of high rates of ecosystem respiration and the development of internal convection cells that can mix the ground level air with air in the mid-canopy. Lloyd et al. (1996) estimated that in the early morning, 6.00–9.00 a.m., a high proportion of the CO₂ molecules in the canopy are of respiratory origin (between 7 and 25%), much higher than occurs in a Siberian coniferous forest. Thus, in the early morning the leaves will experience high CO₂ and they re-fix a significant part of it.

This canopy microclimate is altered when the forest becomes fragmented, by logging or clearing for agriculture. We will return to this later.



Fig. 17.3 Profiles of CO_2 in the canopy for a typical day/night at Reserva Jaru, Rôndonia, Brazil. Local time is shown on the labels e.g. 15h is 1500 hours. From Kruijt et al. (1996)

17.3 Physiological Attributes

The leaves of rain forest trees and seedlings have rates of photosynthesis that are similar to their counterparts in deciduous temperate forests, though possibly slightly lower on average (Chazdon and Field 1987; Riddoch et al. 1991; McWilliam et al. 1996; Carswell et al. 2000b; Domingues et al. 2005; Meir et al. 2007; cf. Sect. 4.5.2 in Chap. 4 by Kutsch et al., and Chap. 6 by Messier et al., this volume). Maximum photosynthetic rates of leaves are generally correlated to the foliar nitrogen content (Wong et al. 1979), and tropical rain forests are considered to be relatively wellsupplied with nitrogen so therefore might be expected to have high rates of photosynthesis (Reich et al. 1994). However, photosynthetic rates in the rain forest, measured under natural light and at ambient CO₂ concentration, seldom exceed 12 μ mol CO₂ m⁻² s⁻¹ (Reich et al. 1994; Carswell et al. 2000a; Dominguez et al. 2007). Exceptions may be the fast-growing pioneers like Cecropia (Bazzaz and Pickett 1980; Reich et al. 1995; Ellsworth and Reich 1996). Sometimes the broadleaved species of temperate regions, when not stressed, have light-saturated rates exceeding 12 μ mol CO₂ m⁻² s⁻¹ (Bassow and Bazzaz 1998; Kull and Niinemets 1998; Raftoyannis and Kalliope 2002). Attempts to compare world-wide photosynthetic rates suggested that leaves of tropical trees may have somewhat lower stomatal conductances than deciduous temperate trees, but the differences are not large (Schulze et al. 1994; Reich et al. 1999; Wright et al. 2004). The physiological characteristics of the leaves also show vertical profiles in the capacity to photosynthesise, and some physiological differentiation into 'sun leaves' and 'shade leaves', much as reported in broadleaved trees from the temperate zone (Meir et al. 2002). When comparisons are made carefully, and at different heights in the canopy, it appears that maximum carboxylation rates from tropical rain forests are somewhat lower than for broadleaved temperate species (Fig. 17.4), despite the fact that these leaves may have relatively high nitrogen contents on an area or mass basis (Meir et al. 2007). These lower rates may be the result of adaptations for survival for longer periods: most leaves in the rain forest canopy are retained for 1–4 years instead of a few months (Reich et al. 2004), and to survive attack by biological agents especially insect herbivores they may require adaptations such as thick cuticles and high levels of plant secondary compounds (Coley and Kursar 1996), with corresponding reduced investment in photosynthetic machinery. In-



Fig. 17.4a–d Leaf-level gas exchange characteristics within forest canopies. Quantities are: **a** V_a maximum carboxylation rate on an area basis, **b** J_a maximum electron transport capacity on an area basis, **c** R_{da} leaf respiration on an area basis, **d** V_m maximum carboxylation rate on a leaf mass basis. From Meir et al. (2002)

deed, Reich et al. (1999) have shown a strong negative relationship between the longevity of leaves and their capacity to photosynthesise. On the other hand, the lower rates may be the result of a shortage of phosphorus: several studies now suggest that phosphorus rather than nitrogen limits the photosynthetic capacity of the leaves of rain forest species (Meir et al. 2007; Kattge et al. 2009), although the overall productivity may nevertheless be limited by the nitrogen supply in many cases (LeBauer and Treseder 2008).

At canopy level, the response of gas exchange, measured by the micrometeorological technique of eddy covariance, is quite similar to that found in deciduous temperate forests, with maximum rates of ecosystem gas exchange in rain forests of $15-25 \ \mu\text{mol}\ \text{CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ (Grace et al. 1995; Malhi et al. 1998; Carswell et al. 2002; Saleska et al. 2003). The important difference is that the rain forest functions more or less continuously all year, whilst temperate deciduous forests shed their leaves in the winter, and boreal forests cease photosynthesis in the cold dark winters. Thus, when annual totals are compared, the rain forest has about twice the annual total of photosynthesis, a consequence of photosynthesising for 12 instead of about 6 months (Malhi et al. 1999; Luyssaert et al. 2007). This is not to say that rates are constant all year: they are likely to vary according to the length of the 'dry season' and are probably influenced greatly by variations in solar radiation and temperatures (Carswell et al. 2002; Saleska et al. 2003). When the estimated productivity of all rain forests are summed, it is thought that they contribute about one-third of all the terrestrial biological productivity of the world (Roy et al. 2001).

17.4 Are Rain Forests Carbon Sinks?

The net ecosystem exchange is the balance between the CO_2 entering the ecosystem by photosynthesis and the losses by autotrophic and heterotrophic respiration. A basic postulate, often heard, is that old-growth forests are carbon neutral, i.e. gains by photosynthesis are equal to losses by respiration. This view is perhaps forged in the ecological paradigm that assumes a process of ecological succession that leads to a 'climax forest' in equilibrium with a more-or-less constant climate. Nowadays we know that the climate fluctuates considerably and has always done so, and we also are more aware that forests are disturbed and most are in a stage of recovery from damage. The circumstances whereby an old-growth forest might be a sink would be in a trend of an increasingly favourable environment that stimulates photosynthesis more than respiration and consequently accumulates carbon, above- and/or belowground. Several authors suggest this can occur as a result of elevated CO_2 or N-deposition (Taylor and Lloyd 1992; Lloyd and Farquhar 1996). Taylor and Lloyd (1992) first devised a very simple theoretical model to show how this depends on the extent of the stimulation and the turnover rate of the carbon pools. Later, Lloyd and Farquhar (1996) made 'reasonable' assumptions and showed how rain forests might accumulate carbon at a rate of around $0.6 \text{ t C ha}^{-1} \text{ year}^{-1}$.

In fact, rain forests in Amazonia have been shown by direct measurement to be acting as carbon sinks (Grace et al. 1995; Malhi et al. 1998). These results were strongly challenged by Saleska et al. (2003), who reported a case where a rain forest was apparently a net source of carbon, using essentially the same measurement technique as the previous authors. However, the same forest moved towards a sink over a period of 4 years, and is now considered to have been recovering from disturbance (Hutyra et al. 2007). There are uncertainties in eddy covariance measurements, especially at night, and it is now clear that the technique has a tendency to under-record night respiration and thus to exaggerate the size of the sink. Moreover, because it is known that spatial variations in the carbon balance of rain forests are large, and in some areas the forest may still be recovering from disturbance, there is always a large sampling problem. Consequently, the issue of whether the Amazonian rain forest *as a whole* is a sink cannot be resolved by eddy covariance alone (Araújo et al. 2002; Kruijt et al. 2004; Rice et al. 2004; Miller et al. 2004; Ometto et al. 2005; Sierra et al. 2007). Rather, it is necessary to deploy other methods as well.

Another way to assess whether ecosystems are carbon sinks is by thorough repeated inventory, involving many sample plots, over a decadal time scale. By showing increases in above ground biomass of up to 0.5 t C ha⁻¹ year⁻¹, analysis of large scale inventories of aboveground biomass have also suggested the rain forests are indeed a sink (Phillips et al. 1998, 2004; Baker et al. 2004). Of course, this approach neglects to study changes in the soil, which may be quite significant. A third way is by analysis of atmospheric CO₂ concentrations, and inferring what the land surface must have been exchanging with the atmosphere to give the observed concentrations. However, this approach also suffers from insufficient sampling densities; although the recent indications it provides suggest a carbon sink in the tropics (e.g. Rödenbeck et al. 2003; Stephens et al. 2007). Clearly, the four approaches - modelling, eddy covariance, forest inventory and atmospheric inversion - all have their own particular weaknesses and are subject to errors that sometimes compromise the estimate; nevertheless, they are completely independent techniques and they point to the same conclusion – that the tropical rain forest is a carbon sink. Is it possible that all these forests are sinks because they are responding to elevated CO₂? Although Clark et al. (2003) demonstrated a statistical correlation between tree growth at one site in Central America and atmospheric CO₂ concentrations as measured at Mauna Loa, it seems unlikely that rain forests are especially stimulated by elevated CO_2 . In other nature forest ecosystems where it has been possible to carry out long term fumigation with twice-normal CO_2 , the enhancement of growth has been hard to detect (Asshoff et al. 2006).

Moreover, Carswell et al. (2000a) showed seedlings of two rain forest species to be rather unresponsive to twice-normal CO_2 , although a greater response was found for a (temperate) liana species by Granados and Körner (2002) and Zotz et al. (2006). There is a possibility that rain forests are responding to long-term trends in other factors. Malhi and Wright (2004) found that since 1970, the rainfall in the humid tropics as a whole has declined by 1%, the N-deposition has increased by 10% and the CO_2 concentration has increased by about 20%. The decline in rainfall

was probably associated with an increase in solar radiation, and that may have been beneficial.

Another way in which carbon fluxes might change is through shifts in species composition over periods of several decades ('long term'). Given that climate and CO_2 has changed over the last century or so, it is possible that changes in species composition will show up in data from permanent sample plots.

17.5 Are There Recent Changes in Species Composition?

The analysis of forest inventory data to test the hypothesis that species composition is changing is a long term project in several centres that is still in progress. There are strong indications of gradients, determined by moisture and nutrient availability, at a regional scale (ter Steege et al. 2006; Swaine and Grace 2007). One indication from the literature is that lianas are increasing in abundance (Phillips et al. 2002; Wright et al. 2004). It is difficult to generalise about the relevant features of lianas because they are taxonomically diverse. However, they have very deep roots and an efficient water transport system (Holbrook and Putz 1996; Restom and Nepstad 2004; Cai 2007; Swaine and Grace 2007). Those in the top of the canopy a have a lower stomatal conductance than trees, and a correspondingly higher δ^{13} C value (Domingues et al. 2007). Schnitzer (2005) examined floristic data from 69 tropical forests worldwide and found a negative correlation between mean annual precipitation and liana abundance. He found that lianas grew seven times faster than trees in the dry season, and twice as fast during the wet season, and attributed this to the tendency of lianas to produce deeper roots than trees. More recently, an examination of the floristics along a rainfall gradient in Ghana, showed that the abundance of liana species (as a proportion of the total species) increased linearly with dryness (Fig. 17.5, from Swaine and Grace 2007). According to Londre and Schnitzer (2006), lianas succeed in disturbed regimes and fragmented forests affected by fire. We may hypothesise that part of the response to a drying trend in the climate might be an increased contribution to the carbon balance by lianas. This hypothesis should now be tested in other regions of the tropics. The implications of a lianaenriched canopy are not clear, but there could be strong feedbacks for the light climate at the forest floor, the microclimate in general and the interaction with the climate system.

17.6 How Will Rain Forests Behave in a Hotter and Drier Climate?

There are rather few studies where it has been possible to measure the growth rates of rain forest trees by repeated annual measurements on the same individuals, and then relate the trends to climatological variables. Inevitably, these studies have a rather small sample size and need to be taken as 'indicative' at this stage. Clark



Fig. 17.5 Liana (•), tree (\circ) and herb (\Box) species as a percentage of all species in 154 sample plots on a rainfall gradient in Ghana (Swaine and Grace 2007)

et al. (2003) examined the diameter growth of six species in Costa Rica, and found evidence for a decline in growth rates associated with increasing night temperatures. More recently, the data of Feeley et al. (2007) from Panama and Malaysia show a negative correlation with minimum temperature, and a positive correlation with precipitation. It seems highly likely from these two examples that warming will reduce the growth rates.

Another line of evidence comes from eddy covariance. The technique enables an exploration of the short-term patterns of CO_2 flux into, and out of, whole ecosystems. Based on data from a forest in southwest Brazil, Grace et al. (1995) showed that the gas exchange of rain forest may be expected to depend critically on temperature and irradiance. The sensitivity to temperature results from the empirical observations of a very strong dependency of plant and soil respiration on temperature, and a non-saturating relationship between incoming solar radiation and canopy gas exchange. A small increase in temperature (1°C) in model simulations was enough to turn the carbon balance from a carbon sink to a source. Thus, one would expect that interannual variability would have a very large impact on carbon balance. Later authors came to a similar conclusion using more sophisticated models (Cramer et al. 2001; Tian et al. 1998; Cox et al. 2000). The model of Tian et al. (1998) additionally showed a high sensitivity to precipitation. The paper

by Cox et al. (2000) is especially interesting, as it is the first in which a simple carbon cycle model has been coupled to a global circulation model (HADCM3) -HADCM3 estimates the climate and ecosystem carbon fluxes of the next 100 years. Large scale climatic phenomena such as the El Niño-Southern Oscillation ('El Niño') are emergent properties and, in this model, the El Niño development is especially strong. The coupled model predicts that the warming of the Amazon will be so large as to trigger a replacement of rain forest by savanna (Cox et al. 2000). However, other models are less conclusive (Friedlingstein et al. 2006). Nevertheless, large El Niños, with an impact on the Amazon forest, may have happened several time since the Holocene. Meggers (1994) found evidence for such phenomena at 1,500, 1,000, 700 and 450 years before the present, and periods of rain forest extinction and re-emergence have been identified in the pollen record from lake sediments (Whitmore 1998; Mayle et al. 2007). The difficulties in modelling the process of rain forest decline relate to our uncertain knowledge of the controls of microbial respiration (Trumbore 2006; Davidson and Janssens 2006), phenology (Hutvra et al. 2007), and fire.

The fire effect is likely to be paramount, and is linked to disturbance and fragmentation. It is well known from field measurements that when rain forest is fragmented, the canopy microclimate is affected, and necromass becomes drier and thus more prone to burning (Kapos 1989). Laurance and Williamson (2001) presented a speculative hypothesis to draw together our knowledge of the interactions between people, fire, forests and climate (Fig. 17.6). Dense forests have a characteristic microclimate with high humidities and daytime temperatures that are lower than those at the top of the canopy. At forest edges the situation is different, with free horizontal ventilation and mixing of canopy air with air from outside.



Fig. 17.6 Conceptual model of the positive feedbacks in the interactions between global warming, humans and deforestation. *ENSO* El Niño-southern oscillation. From Laurance and Williamson (2001)

When drought occurs, relatively dry air penetrates the canopy, and reductions in humidity and increases in plant mortality have been measured at up to 100 m from the canopy's edge (Benitez-Malvido and Martinez-Ramos 2003). Humans light fires, and these fires are likely to ignite more easily and spread more rapidly in the dry conditions of the forest edge. Hence, the forest is damaged and possibly destroyed at a faster rate than would occur in the absence of humans. Such processes have been implicated in the conversion of rain forest to Savanna at a large scale (Bowman 2000). The processes involved are quite complex and collectively amount to a strong positive feedback. In the Laurance–Williamson model, deforestation causes less evaporation, which in turn leads to less rainfall and hence droughts are exacerbated (Laurance and Williamson 2001). Logging can also be important as it thins the canopy and increases vulnerability to combustion.

17.7 The Future

17.7.1 A Pessimistic View of the Future

The dynamics of old-growth forest are likely to change as the environment changes. It is easy to see how it might happen: the duration of the dry season is likely to increase and impact negatively on biodiversity; occasional severe droughts will become more common and lead to extensive forest fires; the encroachment of people into the forest will lead to attrition exacerbated by the processes proposed by Laurance and Williamson (2001); the carbon cycle will be impacted and the tropical regions will rapidly become a source of carbon to the atmosphere. The effects of loss of forest area will alter the albedo and the water balance of whole regions and, through teleconnections, this will impact upon the climate in other parts of the world (Werth and Avissar 2002). So far, coupled climate and vegetation models are at a primitive stage of development and they provide insufficient insight into how soon the changes may occur. Truly useful areas of research are rather difficult to define, but it is clear that the general vegetation–atmosphere linkage is still poorly understood, and more work is needed in many areas before we can make good predictions.

17.7.2 An Optimistic View of the Future

On the other hand, if fossil fuel emissions are less extreme than suggested by predictions (IPCC 2007), and if the Cox et al. (2000) model-prediction turns out to be pessimistic because of the rather coarse assumptions made in that model about heterotrophic respiration, we may expect a different outcome. Rain forests would still be degraded to a large extent, but secondary rain forest has useful

characteristics (Brown and Lugo 1990). If the global CO_2 concentration could be held at 550 ppm and the temperature increase to 1°C, and if measures for forest protection at a global scale were stronger, we might preserve much of the rain forest and some of the environmental services it provides. Forest protection might be achieved by extending the terms of the Kyoto Protocol to include not just 'afforestation' but also 'avoided deforestation' (cf. Chap. 20 by Freibauer, this volume), especially if this is linked to the development of carbon-cycle surveillance techniques using advanced satellite remote sensing techniques, which are already developing fast (Xiao 2006; Grace et al. 2007; Chap. 18 by Achard et al., this volume). Essentially, this means that many poorer countries of the world would be paid for keeping the rain forest intact for the benefit of the Earth and humankind.

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