5

TROPICAL FORESTS

Lindsay F. Banin, Oliver L. Phillips and Simon L. Lewis

Introduction to tropical forests

Tropical forest ecosystems occur between the tropics of Cancer and Capricorn (23.5° N and S of the Equator, respectively) and are characterized by dense, relatively tall, closed canopies with trees making up the dominant life form in structurally complex arrangements. Tropical forests are amongst the most speciose systems on the planet, in terms of both flora and fauna, and are estimated to contain more than half the world's recorded species. They deliver important ecosystem services, such as large-scale cycling of carbon and water, and more locally, through the provision of clean water, shelter, food and fuel to local populations. At the global scale, their limits are determined by climate and at smaller spatial scales, their presence and form is determined by local or regional topographic, geological and edaphic features, as well as anthropogenic impacts.

There is no consistent, universal definition of 'tropical forest' (see Torello-Raventos *et al.* 2013), and this is due largely to the fact that classification boundaries are drawn somewhat arbitrarily along ecological gradients; vegetation types grade from one to another along environmental continua (Woodward *et al.* 2004). Yet, it is clearly useful to define ecosystems for robust temporal and spatial comparisons and decision-making (Putz and Redford 2010). There are numerous global-scale vegetation classification schemes (e.g. Köppen 1923; Holdridge 1947; Whittaker 1975). Vegetation is classified into biomes which indicate the major ecological communities present over extensive regions of the world. Biomes correlate well with climatic regimes but are independent of floristic assemblage. The structural and functional attributes of the vegetation relate to physiological constraints on the resident communities, giving rise to similar physiognomy amongst continents.

Length and intensity of dry season are strong determinants of forest occurrence and form (Zelazowski *et al.* 2011). Tropical rain forest occurs where rainfall is abundant (approx. > 1,800 mm annually) and well-distributed throughout the year with no notable, or at most a short, dry season. Vegetation is evergreen and dominated by trees, with other life forms including lianas, epiphytes and ~~tree~~ ferns. As seasonality increases, tropical dry forests (which are also commonly referred to as monsoon forests, seasonally dry forests, deciduous or semi-deciduous forests) occur where there is a pronounced, regular dry season, during which some, many or all of the trees shed their leaves. Dry months are often defined as when

precipitation falls below 100 mm – the estimated potential evapotranspiration rate of most lowland tropical forests (Shuttleworth 1988).

Tropical forests occur in a band around the equator; Central and South America constitute the neotropics and Central, West and East Africa, Madagascar, South and Southeast Asia, Papua New Guinea, Melanesian islands and Australia make up the palaeotropical region. Currently, the largest contiguous tracts occur in South America (the Amazon basin), Central Africa (the Congo basin) and Papua New Guinea. Altitude has also been shown to be an important determinant of forest structure and physiognomy, mostly because of the decline in temperature (lapse rates average ca. 6°C per 1,000 m elevational difference) and hence tropical montane forest is regarded a distinct and separate formation. Locally, other distinctive forest formations arise from underlying geology, soils and proximity to water, such as coastal mangroves, peat swamp and gallery forests.

Vegetation classifications are determined by climatic envelopes and represent *potential* cover rather than *actual* cover. More recently, developments in remote sensing and geographical information systems have meant that large-scale vegetation cover can be observed using information from satellites. Estimates based on SPOT-4 VEGETATION satellite data (Global Land Cover 2000 product, see Mayaux *et al*. 2005; Bartholomé and Belward 2005) indicated that tropical moist forests (delimited following the FAO definition of 0–3 dry months, when rainfall is less than twice the mean temperature) occupy approximately 1,100 million hectares, or roughly 10 per cent of vegetated land cover globally. South American forests constitute more than half (58 per cent) of the total tropical moist forest cover, African and Asian forests contribute ~20 per cent each whilst forests in India and Australia occupy relatively small, isolated tracts where the local climate and soils permit (Mayaux *et al*. 2005). Remotely sensed data can be used to estimate changes in areal cover, but still rely on consistent definitions of what constitutes 'a forest' (see Box 5.1).

Box 5.1 Disturbance and management history of tropical forests

Forests can take many forms depending on their disturbance and management history. Putz and Redford (2010) propose the following classification scheme. Old-growth forests (sometimes referred to as primary, pristine, virgin or intact) are largely unmodified by human activities and can be determined by tree age and size distributions, number of canopy layers and species composition. Degraded forests have been modified by logging, overhunting, fires or species invasion and have lost some structural or compositional elements of old–growth forests. Secondary forests are those which have regenerated following clearance. Degraded and secondary forests represent a large proportion of tropical forest cover and there is an increasing awareness of their ecological value. Plantations include intensively managed tree farms (e.g. oil palm, rubber). By contrast, managed forests include planted stands of native trees which may permit native understories. Natural or semi–natural disturbances (including hurricanes and fires) can also 're-set' the successional status of a forest.

Physical geography of tropical moist forests

In a global context, the tropical forests are often treated as a uniform entity yet there is distinct variation in important biophysical variables (precipitation, temperature, incoming solar

radiation and soil conditions) which have profound effects on spatial patterns of forest form and function.

Precipitation and its intra- and inter-annual seasonality

Precipitation varies over regional scales, both in terms of total annual rainfall and the seasonality of rainfall, with the lowest mean annual precipitation occurring in regions with strong intra–annual seasonality. Precipitation is largely determined by latitudinal distance from the equator; dry seasons are strongest and longest with increasing distance due to seasonal shifting of the inter-tropical convergence zone (ITCZ) (McGregor and Nieuwolt 1998). These patterns are modulated by atmospheric circulation patterns and local geography, including distance from the sea, coastline orientation and orography. On average, mean annual precipitation is highest in northwest Amazonia, Southeast Asia and New Guinea (~2,500 mm per year) where there is no regular, annual dry season and lower in Africa, South Asia and Australia (Figure 5.1a).

In the neotropics, a large gradient in rainfall is observed (Figure 5.1a). The wettest regions are close to the equator, receiving rainfall throughout the year from the ITCZ air masses, and regions on the east-facing slopes of the Andes due to orographic uplift of easterly winds (McGregor and Nieuwolt 1998). Dry seasons occur in Central America and both northern and southern fringes of the Amazon basin and these tend to be most intense in southeast Amazonia.

Mean annual precipitation is generally lower in African tropical forests where almost all regions experience a dry season (Figure 5.1a; ~ 1,800 mm per year). Some areas are subject to one longer dry season (~10°N and S) but most tropical forests in Africa receive two less intense dry periods, one when the ITCZ is furthest north (July–August) and another longer one when it is furthest south (December–March) (McGregor and Nieuwolt 1998). Geography also has an effect in West Africa; Ghana and Côte d'Ivoire receive less rainfall since their coastlines are parallel to onshore winds, and are in the rain shadow of the Liberia and Sierra Leone coastlines.
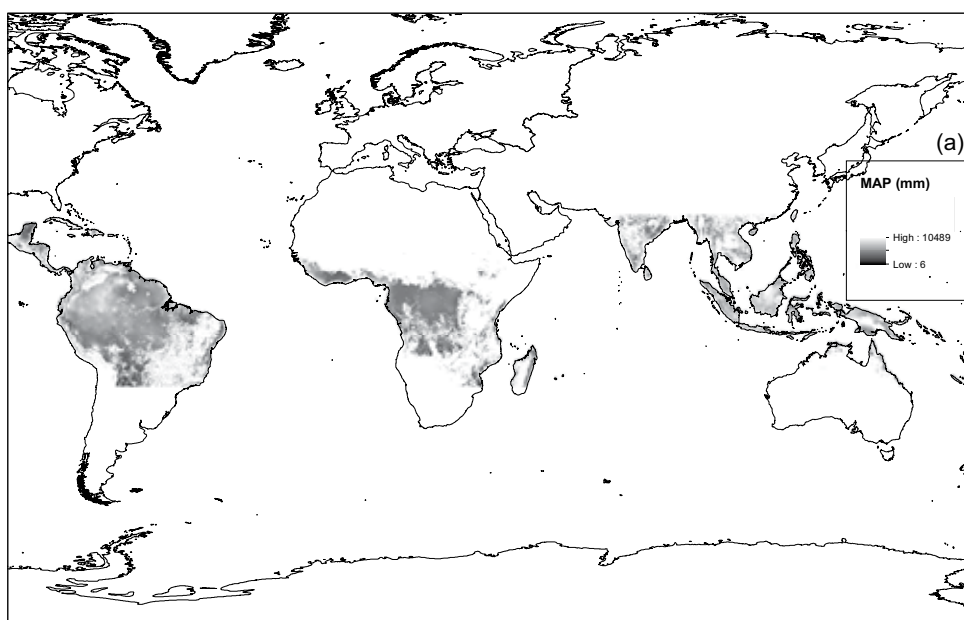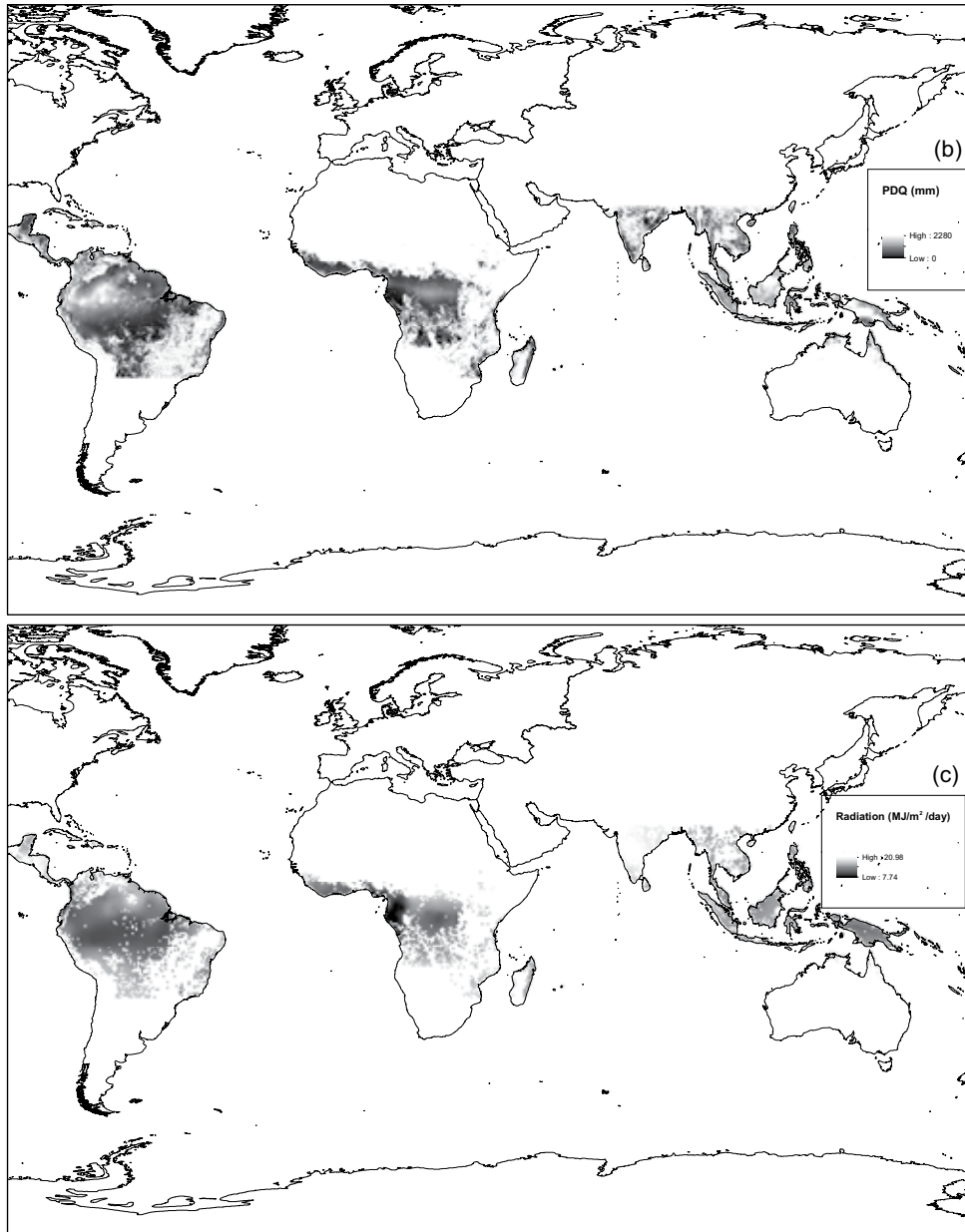
Figure 5.1 Map of (a) mean annual precipitation (mm), (b) precipitation in driest consecutive three months (mm) and (c) solar radiation (megajoules per metre squared per day) for the tropical forest regions. Shading represents satellite-derived Global Land Cover 2000 classes: (1) broadleaved evergreen closed to open trees; (2) broadleaved deciduous closed to open trees; (7) broadleaved evergreen closed to open trees on flooded land and; (17) mosaic cultivated/managed terrestrial areas and closed-open trees (Mayaux *et al.* 2005; Bartholomé and Belward 2005) within 23.5°N and S of the equator. Rainfall data are from the WorldClim datasets; interpolations of climate station data to 30 seconds spatial resolution (a, b; Hijmans *et al.* 2005) and radiation based on interpolations of sunshine hours and/or cloud cover at 0.5° resolution from Climate Research Unit (c; New *et al.* 1999)

The effects of lower rainfall in African forests are however moderated by the relatively higher elevation and lower temperatures (Malhi and Wright 2004).

The climate in tropical Asia is driven by the Indo–Australian monsoon systems and modified by local orography (Walsh 1996b). Precipitation is high in insular Southeast Asia, the Malay Peninsular and Papua New Guinea (Figure 5.1a) where monsoons deliver rain throughout the year, although drier periods occur in different regions at different times in association with surface features (Walsh 1996b). In South Asia, a short dry season occurs in the forested southern Sri Lanka, whilst the Indian and Thai forests receive much of their rain between July and September (McGregor and Nieuwolt 1998). Conversely, the wet season south of the equator in south-eastern Indonesia, southern New Guinea and northern Australia occurs from ~~in~~ December to March, during which Australian forests receive 60–90 per cent of their annual total (Figure 5.1b). Orography influences local rainfall patterns; the eastern facing slopes of the Great Dividing Range capture most of the rains, and the mountains forming a central ridge across Papua New Guinea produce a rain shadow to the south of the landmass (McGregor and Nieuwolt 1998).

Anomalies in sea-surface temperature can create inter-annual variability in rainfall where some regions of the tropics are subject to periodic, sometimes very severe, drought. The El Niño Southern Oscillation (ENSO) particularly affects South America and Asia. The 'Southern Oscillation' refers to the coupled shift in sea-surface temperature and atmospheric pressure that occurs in the Pacific Ocean roughly every three to five years. Under 'normal' conditions, high sea-surface temperatures in the western Pacific bring rainfall to Southeast Asia. During El Niño conditions, easterly trade winds slacken, allowing warmer water to propagate eastwards to the central and eastern Pacific. As a result, the large-scale distribution of atmospheric uplift and descent changes around the globe. Drier than usual weather (associated with descending air) prevails in Australia, New Guinea, Malaysia and north Brazil and the Guyanas, and sometimes East Africa. The western coast of South America is one of the areas receiving greater rainfall during El Niño events. During the opposite phase (La Niña) the trade winds strengthen and warm waters move west, changing rainfall patterns. The Atlantic Multidecadal Oscillation (AMO) refers to sea-surface temperature anomalies in the Atlantic and is associated <mark>withreduced</mark> rainfall, this time in the south and west regions of Amazonia. These inter-annual droughts are known to reduce plant growth and increase tree mortality through fatal embolism in affected forests (Phillips *et al.* 2010). They also increase risk of large forest fires which have occurred in Amazonia and Indonesia in recent years.

Temperature and altitude

Lowland tropical forests are highly productive compared with other terrestrial ecosystems because the warm environment sustains year-round growth. In the lowland tropical rain forest regions, mean annual temperature is high (> 18°C) and there is little seasonality since the sun is almost overhead throughout the year. Diurnal variations in temperature tend to be stronger than seasonal ones, although temperatures can rise during dry seasons due to the lack of cloud cover (Walsh 1996a). Variation in altitude is the primary driver of differences in temperature across the tropics. Africa and Australia's lowland ~~(< 1,000 m above sea level)~~ forested regions are at higher altitudes on average, resulting in lower regional mean annual temperatures than in tropical America and Asia, allowing forests to persist where lower rainfall would otherwise be prohibitive.

Radiation and cloud cover

Solar radiation in the tropics is largely determined by cloud cover and the diurnal timing of rainfall, which itself depends on proximity to oceans, location in relation to wind direction, coastal geometry and orography (Walsh 1996a; Churkina and Running 1998). Maritime settings tend to receive rainfall at night as a result of night–time temperature differences between surface air warmed by the oceans and the radiative cooling of cloud tops whilst continental regions have a greater amount of rainfall during the day, in association with the peak in land heating and convection (Walsh 1996a). Coastal regions with steep elevation also tend to receive rainfall in the daytime as a result of orographic uplift of sea breezes; this is the case in some coastal regions of West Africa and the mountain range on the east coast of Australia (McGregor and Nieuwolt 1998). Annual averages of solar radiation may also be affected by seasonality in cloud cover; regions experiencing strong dry seasons will have periods of high incoming solar radiation.

Mean solar radiation, calculated from standardized sunshine hours and/or cloud cover data (Figure 5.1c) is notably higher in tropical Asia and Australia compared with America and Africa. Insular Southeast Asia receives much of its rainfall at night, whereas America and Africa on the whole are subject to a continental regime in diurnal rainfall.

Climate change in the tropics

In the tropics, surface air temperatures have been rising by 0.25°C per decade for the last 30 years (Malhi and Wright 2004). Model projections indicate that the temperature of tropical forest regions will increase by at least 2–4°C by 2100, dependent on future greenhouse gas scenarios (Williams *et al.* 2007). As the tropics encompass the warmest climate on earth, this change will generate novel climates and thus it is difficult to predict how biota will respond – the physiological tolerance and adaptability of tropical species to warmer temperatures is largely unknown, particularly as they have evolved in regions where seasonal variation is limited (Williams *et al.* 2007; Wright *et al.* 2009; Corlett 2011). Plants are likely to be able to tolerate small changes in temperature alone through adjustments to stomatal conductance and due to the simultaneous increased concentration of CO_2 (Lloyd and Farquhar 2008). Heat damage to leaves can occur for temperatures in excess of 4°0°C which are plausible at the top of the canopy, particularly if solar radiation is high, and thus seasonally dry forests could be particularly vulnerable (Corlett 2011).

Whilst there is high confidence that warming will occur in all tropical regions, there is greater uncertainty around projections of changes in precipitation. Precipitation trends in recent decades have been less clear than those of temperature, the natural variability is less well defined and the modelling of monsoons and inter–annual climatic events such as ENSO presents significant challenges (Christensen *et al.* 2013; Li *et al.* 2011). The IPCC AR5 report (Christensen *et al.* 2013) outlines the projected regional differences in precipitation trends at the end of the century under a given greenhouse gas emission scenario. In South America, changes in annual precipitation are not anticipated but increases in the variability and extremes of precipitation are projected. Dry–season rainfall is expected to decrease in east Amazonia, and north–east Brazil, whilst positive extreme precipitation trends may occur on the north–west coast, Peru and Ecuador. A reduction in warm–season precipitation is also projected for Central America and the Caribbean. There has been some evidence of drying in west Africa in recent decades (Fauset *et al.* 2012), but model–based projections of future precipitation trends are highly uncertain (Christensen *et al.* 2013). Little change in annual precipitation is projected for East

Africa, though the annual distribution may alter. The complexity of geography and terrain in South and Southeast Asia complicate projections for this region; moderate increases in rainfall are projected for most parts Southeast Asia and summer monsoon precipitation may increase in South Asia. Changes associated with ENSO remain uncertain in both Southeast Asia and Australia. Increased seasonality in rainfall may also occur in Australian tropics, due to decreases in the strength of westerly winds to the north (Christensen *et al.* 2013). The projections focus on changes at one snapshot of time, yet changes may be dynamic over time and not unidirectional – some regions may first get wetter and then drier, according to changes in the position of the ITCZ (Hawkins *et al.* 2014).

Whilst the impacts of climate change on tropical vegetation are uncertain, warmer temperatures may lead to upslope migration of some species (Feeley *et al.* 2011) – this could, of course, be problematic for species where this option is not available. Reduced rainfall may lead to the expansion of tropical dry forests or savannas into regions that are currently occupied by tropical rain forests, for example in eastern Amazonia (Malhi *et al.* 2009). Higher temperatures, coupled with reduced rainfall and greater human influence may mean that these forests are more susceptible to fires. Changes in forest cover may also induce ~~positive~~ feedbacks – tropical forests generate clouds via transpiration, and thus are a major regulator of regional weather. As forest cover is reduced, this hydrological cycling may break down leading to further drying and forest loss.

Soil and geology

Soils of the tropics are typified by old, deeply weathered and nutrient poor profiles, due to the hot, humid climate which promotes erosion and leaching. However, soil characteristics are determined by five key factors: substrate geology, topography and drainage, climate, age and biota (Jenny 1941), leading to heterogeneity at local, regional and continental scales. Commonly-occurring soils in the tropics are presented in Table 5.1. Various soil classification schemes exist; here we use the World Reference Base for Soil Resources (WRB) nomenclature (IUSS Working Group WRB 2006). Geological development of the major tropical forest regions ultimately determines the age and composition of soils. Three principal geological landforms exist across the wet tropics: i) the ancient Precambrian shield areas or 'cratons', making up large parts eastern South America, equatorial Africa, and central and southern India which yield deeply weathered Ferralsols characteristic of the tropics; ii) the alpine fold belts comprising much of Southeast Asia, the Andes and Central America, eastern Australia and northern Papua New Guinea, and; iii) the alluvial plains of the Amazon and Congo basins and the coastal plains of the Guyanas and Mekong and Niger deltas (Beckmann 1983; IUSS Working Group WRB 2006). These landforms drive large-scale variability in soil characteristics which are modulated locally by variations in geology, topography, drainage and organisms.

There is a strong east-to-west gradient in geology and soil in South America. Central and eastern Amazonia is underlain by Precambrian shield and well-weathered, nutrient poor Ferralsols predominate. The strong topography of the Andes promotes erosion so that new, unweathered surfaces of parent material are continuously exposed, replenishing nutrients in the surface soil. Thus, in general, the soils are more fertile in the west ~~than the east~~, comprising Leptosols and Regosols at the upper-most elevations and a mixture of Andosols, Cambisols, Luvisols, Acrisols and Alisols at lower elevations (Irion 1978; Quesada *et al.* 2012a). Floodplain soils (Fluvisols and Gleysols) flank the Amazon River (Quesada *et al.* 2012a).

Precambrian shield regions predominate in West Africa and form a rim around the Congo basin. The central basin itself and some parts of West Africa are made up of sediments with

Table 5.1 Dominant tropical soil groups by WRB classification, organized by primary forming factor. Descriptions are based on IUSS Working Group WRB (2006), Quesada *et al.* (2012a) and Dudal (2005)

Soil group	Distinguishing features	Typical nutrient status
Limited age		
Leptosols	Shallow soil over hard rock/gravel, usually at medium to high altitude	Dependent on parent material Accumulation of carbon
Cambisols	Horizon definition only beginning, with slight to moderate weathering of parent material. Found on erosional surfaces	Dependent on parent material
Climate		
Acrisols	Sub-surface accumulation of low activity clays and low base saturation	Low
Alisols	Sub-surface accumulation of high activity clays (smectite and vermiculite)	Moderate, but with Al concentrations
Ferralsols	Deep, strongly weathered, physically stable but chemically depleted	Low
Lixisols	Soil with high activity clay but high in exchangeable bases (in contrast to Alisols)	Moderate–High
Nitisols	Deep, clayey soil with well-defined nut-shaped peds with shiny surfaces. Developed on intermediate to basic substrates	High
Plinthosols	Notable presence of plinthite (Fe–quartz–kaolinite concretions) associated with a fluctuating water table	Moderate
Podzols	Illuviation of Fe, Al and organics, commonly on alluvial/coluvial/aeolian siliceous materials	Low, with high acidity and Al concentrations
Topography and drainage		
Fluvisols	Soils on recent alluvium, often shallow	Variable with parent material
Gleysols	Temporary or permanent wetness near soil surface; gleyic colours and evidence of reduction	Comparatively fertile (but anoxic conditions)
Umbrisols	Occurring at high altitudes. Accumulation of organic matter due to low temperatures and acidic	Bases dominated by high Al concentrations
Parent material		
Andosols	Dark, organic–rich, soils on volcanic materials	Variable with pH
Arenosols	Sandy soil with limited soil development	Low
Luvisol	Unconsolidated alluvial/colluvial/aeolian deposits in cooler environments and young surfaces	Variable with parent material
Vertisols	Clay soils which expand and contract (smectite) to cause cracking	High (but may be physically inhibiting due to dense clay)

restricted areas of basalt from volcanic intrusions and extrusions (Juo and Wilding 1996). Ferralsols, Nitisols and Acrisols are the most extensive soils on both shield and sedimentary substrates. Cambisols and Gleysols are also found in accordance with local topography, and more nutrient rich Lixisols are represented in regions of Ivory Coast, Ghana and Nigeria (Juo and Wilding 1996).

Ancient shield geology only occurs in small, isolated patches in tropical Asia. Much more common are sedimentary and volcanic substrates (Dudal 2005; Hammond 2005). As a result

Acrisols comprise ~50 per cent of the region (Dudal 2005), though Ferralsols and Nitisols on Precambrian shield can be found in India. Vulcanism at the boundaries of the Sunda shelf means that Andosols and Leptisols are more common in Asia (Dudal 2005). Arenosols, formed on ancient coastal and river terraces, are also reasonably well represented. Gleysols, Fluvisols and Cambisols occur according to local conditions.

The soils in north–eastern Australia are heterogeneous due to the variable materials which make up the Great Dividing Range and the patchy distribution of basalt (Hubble and Isbell 1983; Hubble *et al*. 1983). Fluvisols, Ferralsols, Acrisols, Podzols, Cambisols, Lixisols and Vertisols are commonly found in tropical Australia, depending on local geology and site conditions (Table 5.1; Hubble and Isbell 1983; Hubble *et al*. 1983). The northern part of Papua New Guinea is made up of folded sedimentary rocks whilst Precambrian crust underlies southern New Guinea (Hammond 2005). Cambisols, Regosols, Leptosols and Histosols (soils with high organic matter associated with cool environments) are more commonly found in association with the strong topography. Acidic Umbrisols and Histols, both dark with high organic matter content, are also more common. More deeply weathered Acrisols represent regions in the south and Fluvisols, Lixisols and Gleysols are also represented (IUSS Working Group WRB 2006).

In sum, Ferralsols associated with Precambrian shield geology are common in large areas of tropical South America and Africa whereas Asia and eastern Australia are geologically much younger, with Acrisols particularly common in Asia. Data from the Harmonized Global Soil Database (FAO 2008) indicate that the most nutrient poor soils, in terms of total exchangeable bases (TEB: sum of Ca^{2+}, Mg^{2+}, K^+ and Na^+, a common measure of soil fertility) are absent in Asia and volcanic soils are more common meaning that, on average, TEB is higher in Asia than South America and Africa (Huston 2012). Nonetheless, the topsoil of Acrisols in Asian forests can also be very low in exchangeable bases (Banin *et al*. 2014). It is also noteworthy that nutrient availability to plants is not solely determined by the soils they grow in – atmospheric deposition of nutrients from marine sources, dust and anthropogenic activities also contribute and are spatially variable (Townsend *et al*. 2008).

Whilst soils of varying fertility are found in the tropics, in a global context they are overwhelmingly nutrient poor and yet in many localities they sustain the highest productivity of any terrestrial vegetation. This has been attributed to efficient nutrient cycling within the system to avoid losses to groundwater and the atmosphere. Mechanisms for nutrient capture and retention include dense root mats at the soil surface, symbioses with mycorrhizal fungi, algae and lichen, rapid growth of feeder roots, nutrient translocation before leaf abscission and long leaf lifespans and plant defences to prevent loss by herbivory (Stark and Jordan 1978; Jordan and Herrera 1981). In addition to nutrients, physical soil conditions may also be limiting to plants, and these also vary with soil type. Young soils (e.g. Leptosols, Cambisols) and the formation of hardpans and concretions (e.g. in Plinthosols, Podzols and Acrisols) can prohibit deep rooting systems (Quesada *et al*. 2012a). Inundated soils and sandy soils, such as Fluvisols, Luvisols, Gleysols and Arenosols, have poor structure and can be unstable. In all these cases, trees are more susceptible to uprooting. Ferrasols conversely, are typically deep, well-structured and store water effectively, which can be beneficial during periods of drought.

Biogeography and diversity of tropical trees

Tropical moist forests are highly diverse compared with temperate forests, yet there is still a great variety in species richness within the tropics. For instance, African forests are markedly less diverse on average. Present day warm and wet environmental conditions may promote

64

high diversity, but historical biotic exchange and evolution also explain some patterns in species distributions and diversity we see today.

The angiosperm flora that dominates the modern tropics is thought to have evolved in the mid-Cretaceous, coinciding with the break-up of Gondwana, approximately 100 million years ago [Mya] (Lidgard and Crane 1988; Primack and Corlett 2005). The plant species existing within tropical forests on each continent are thought to represent individualized evolutionary responses to the physical environment on each continent, though dispersal routes are also likely to have contributed to the current floristic assemblages (Primack and Corlett 2005; Corlett 2007; Donoghue 2008).

A combination of altered dispersal routes, past climatic changes and modern processes shape the distributions we see today, and several key events are thought to have had a particularly profound effect.

There was a significant drying of the tropical regions ~ 20 Mya and an associated reduction in tropical forest cover (Cox and Moore 2000). The relatively low diversity in African forests has been attributed, in part, to this period of drying and the contraction of tropical forest area. Conversely, relative climate stability coupled with regional-scale water cycling over the Amazon basin is thought to have resulted in high local diversity and low extinction rates in parts of Amazonia (Bush *et al.* 2004). The diversity of South American forests was also hugely influenced by the orogeny of the Andean mountains in the Tertiary and the connection formed with North America via the Isthmus of Panama ~3–4 Mya, initiating the Great American Interchange (Primack and Corlett 2005).

During the last glacial maximum colder conditions prevailed in the tropics; a drop in sea-surface temperatures of ~ 5°C reduced convective rainfall leading to dry episodes (Guilderson *et al.* 1994). It remains contentious whether this resulted in widespread deforestation. The glacial drying was more pronounced in Africa and Australia and led to rapid changes in forest composition. At this time, sea levels were also lower and the islands making up Southeast Asia became land-linked, facilitating movement of species around the region (Giresse *et al.* 1994; Cannon *et al.* 2009). In the neotropics, montane assemblages existed in lowland areas, and thus temperature drove migrations of Andean and Amazon floral elements up and down slope (Bush *et al.* 2004; Kellman and Tackaberry 1997).

Despite long periods of separation, striking similarities occur throughout the modern tropics, particularly in terms of tree familial composition. Using a pan-tropical collation of data from 35 forest plots (see Box 5.2), Gentry (1988) showed that there is a discernible overlap of the most speciose families across continents. The families commonly found in all tropical regions (except for Australia) were ~~Fabaceae~~, Rubiaceae, Annonaceae, Euphorbiaceae, Lauraceae, Moraceae, Sapotaceae, Myristicaceae and Meliaceae. Lauraceae, Myrtaceae and Rubiaceae were also common in Australia. One of the most prominent differences is the dominance of the Dipterocarpaceae in Asian forests, which are largely absent elsewhere, and the comparative dominance of ~~Fabaceae~~ in American and African forests; these two families have been regarded as potential 'ecological equivalents' (Gentry 1988; LaFrankie *et al.* 2006).

Other notable differences in Gentry's (1988) plots between the regions are that i) Bignoniaceae and Arecaceae are more speciose in the neotropics, ii) the Ebenaceae are more speciose in Africa and Asia, iii) Olacaceae and Apocynaceae are more speciose in Africa, iv) Myrtaceae are more speciose in Asia, and the Atlantic Forest of Brazil, and v) Proteaceae, Elaeocarpaceae and Monimiaceae were particularly speciose in Australia. Gentry's (1988) study also demonstrated surprisingly high overlap at the generic level, with 30 per cent of genera in African sites also found in the neotropics, and 23 per cent and 25 per cent of genera found in Asian and Australian forests, respectively, also occurring in the neotropics.

Whilst this chapter focuses on vegetation, there are also marked differences in the faunal communities of tropical forest regions (see Primack and Corlett 2005). These differences could have profound impacts of the floristic communities through key plant–animal interactions such as pollination and seed dispersal.

Box 5.2 Measurement and monitoring of forest inventory plots

Permanent forest plots can be used to describe species composition, quantify structure and biomass, growth, carbon and population dynamics, and to monitor changes in these measures over time. An area is marked out and all trees below a minimum diameter (e.g. 1 cm or 10 cm diameter at breast height, DBH) are identified taxonomically, tagged with a unique identifier and the diameter recorded (Figure 5.2). In subsequent inventories or 'censuses' diameters of living trees are measured again, trees that died are noted, and new trees reaching the minimum threshold are identified and added to the record. Climbers, palms and understory plants may also be recorded and measured. Additional measurements, including tree height, crown dimensions and canopy cover, may be taken and samples of soil or plant material collected. Standardized methods facilitate robust cross-site comparisons. Some large plot networks have used these techniques in many sites, e.g. RAINFOR in Amazonia (Peacock *et al*. 2007), AfriTron in Africa (Lewis *et al*. 2013), CSIRO permanent plots in Australia (Bradford *et al*. 2014) and the pan-tropical CTFS (Centre for Tropical Forest Science) network (Losos and Leigh 2004). In extension to the forest inventory, the GEM (Global Ecosystem Monitoring) network also examines other components of the carbon budget including gas fluxes, root biomass and production and canopy production (e.g. Kho *et al*. 2013). These datasets are collated with the invaluable support and contribution of local institutions and communities.

Figure 5.2 Measuring tree diameters in forest inventory plots. Photo credit: LFB and Jugah Tagi

Tropical forest structure and dynamics

There are discernible differences in the structure and dynamics of forests across the tropics. Here, we particularly focus on findings from ground-based data (Box 5.2) and from old-growth tropical forests which better reveal 'natural' controls, since the functioning of human-modified forests is substantially impacted by their disturbance histories (see Box 5.1).

Structure

Forest structure can be categorized into horizontal and vertical components. Important measures of horizontal structure include stand-level stem density, basal area and stem size distributions. Vertical structure refers to the third dimension and includes canopy characteristics such as tree height, height-diameter relations and crown dimensions and arrangement. Above-ground biomass (AGB) includes both horizontal and vertical components and is the total dry mass of living organic matter, made up of stems and branches, leaves and reproductive organs, whilst below-ground biomass is composed of mostly roots (Malhi *et al.* 2006). To actually measure biomass, trees must be felled so biomass is usually estimated for larger forest areas using allometric equations developed from harvested trees (e.g. Chave *et al.* 2005).

Tropical rain forests are characterized as structurally complex systems, storing and cycling large amounts of carbon in woody tissue, however, structure and biomass are not uniform across the tropics. On average, African forests are made up of fewer, large stems, when compared to South American and Asian forests, whilst stem density is particularly high in Australian forests (Banin *et al.* 2012; Lewis *et al.* 2013). Higher basal area and AGB values have been recorded for forests in Asia when compared with Neotropical and African forests and variation in AGB is closely linked with the abundance of large-diameter trees (Lewis *et al.* 2013; Slik *et al.* 2013). Correspondingly, AGB is greater in central and eastern Amazon, where trees are long-lived and large, than in the western parts of the basin (Quesada *et al.* 2012b). Average maximum tree height and height-diameter relationships also vary: trees attain greater heights and are taller for a given diameter in Asia, Africa and central-east Amazon and are shorter in western Amazon and Australia (Banin *et al.* 2012). These differences are closely related to differences in basal area, mean tree size and tree lifespans. Nonetheless, maximum tree heights operate within mechanical and hydraulic limits (McMahon 1973; Ryan and Yoder 1997). Tropical dry forests are structurally distinct and tend to have lower basal area, AGB and are shorter for a given diameter (Chave *et al.* 2008; Feldpausch *et al.* 2011).

Stock parameters, such as basal area and AGB can be envisaged as the net result of tree growth inputs and mortality outputs. Whilst the relationship between above-ground net primary productivity (NPP; defined below) and AGB is strong and positive across some biomes where growth is seasonally limited, this relationship does not appear to hold for tropical forests (Keeling and Phillips 2007). Here, basal area and AGB are often determined by mortality rather than growth. Across Amazonia, structure follows a general east-to-west gradient with basal area, AGB and maximum height decreasing towards the west (Baker *et al.* 2004; Banin *et al.* 2012). Coincidently, stem dynamics increase towards the west, with higher incidence of tree falls (Chao *et al.* 2009). The varying levels of disturbance-driven mortality is perhaps why large-scale analyses of the determinants of forest structure have yielded different, and sometimes conflicting, results (e.g. Laurance *et al.* 1999; Saatchi *et al.* 2007; Slik *et al.* 2013). In addition, NPP and mortality are correlated and whilst a number of hypotheses exist, the causal relationship is unknown (Stephenson *et al.* 2011).

Growth and production

At the individual plant level, growth can be measured in terms of change in size (frequently diameter in trees) or biomass change (production). Differences in growth and production rates can be due to differences in the genetic composition of a plant, its expression within a given environment and the environmental conditions and interactions with other organisms that it encounters. Plant growth is primarily limited by availability of the key resources water, light, temperature, nutrient availability and atmospheric carbon dioxide concentrations.

Water is essential for plant cell maintenance, biochemical reactions and transport of organic molecules and inorganic nutrients. As we have seen, it is a determinant of tropical forest distribution. Yet, large-scale studies have failed to identify annual rainfall as a primary determinant of above-ground wood and litter production within the wet tropics (e.g. Clark *et al.* 2001; Malhi *et al.* 2004; Chave *et al.* 2010; Schuur 2003). This may be due to two factors: first, it is rainfall in the dry season rather than annual totals that is critical for growth and second, soil water availability exploited by plant roots (determined by water holding capacity, texture and depth) is more important than rainfall *per se*. Overall, the net effect of water availability on stand-level growth and production in tropical moist forests is likely to be greater in regions where dry seasons are long enough for soil water reserves to be depleted. Further, dry periods may actually promote tree growth when soil water is sufficient to buffer the reduction in rainfall, because photosynthetically active radiation (PAR) is a limiting resource in tropical rain forests due to the thick cloud cover (Graham *et al.* 2003; Nemani *et al.* 2003).

Regional studies have identified large-scale correlations between soil fertility and above-ground wood production rates (Kitayama and Aiba 2002; Malhi *et al.* 2004; Paoli and Curran 2007; Quesada *et al.* 2012b; Banin *et al.* 2014). In Amazonia, above-ground wood production (AGWP) varies from ~ 3–11 tonnes per hectare per year (Malhi *et al.* 2004). Whilst climatic factors did not appear to explain this variation, the observed east-to-west gradient of increasing AGWP was consistent with differences in soil fertility.

It is most widely accepted that tropical lowland forests are P limited, and that N is in abundant supply, except in cooler, montane environments and the most nutrient poor sites (e.g. Vitousek 1984; McGroddy *et al.* 2004). A leading explanation for this is based on the observation that plant-available P must be obtained from weathering parent material, and in the old oligotrophic soils which dominate the tropics, P is only present in small quantities. AGWP has been found to be particularly well correlated with soil total P in forests in Amazonia and Borneo (Paoli and Curran 2007; Quesada *et al.* 2012b).

Fertilization experiments have also been used to determine the nature of nutrient limitation on plant growth and production. Responses to the experiments have been variable but increases in sapling and tree diameter growth, litterfall mass and litter nutrient content from a number of studies suggest that plant productivity is limited by nutrient availability in the tropics, but that nutrients other than P may be co-limiting – the base cations, calcium, potassium and magnesium and other micronutrients can also be important for plant growth, functioning and species distributions (Mirmanto *et al.* 1999; Kaspari *et al.* 2008; Wright *et al.* 2011).

Differences in above-ground growth and wood production rates across tropical forest regions are not well known, but rates of AGWP appear to be higher in Borneo than Amazonia (Banin *et al.* 2014).

At the ecosystem level, NPP is the amount of carbon assimilated via photosynthesis (gross primary productivity, GPP) less that lost via autotrophic respiration, and is of key interest in studies pertaining to carbon balance (Del Grosso 2008). NPP is composed of woody structures (stems and branches), foliage, roots, reproductive tissues (flowers, seeds, fruits), production lost

to herbivory, emissions as volatile organic compounds (VOCs), root exudate and supply of carbohydrate to mycorrhizae (Luyssaert *et al.* 2007). Primary production may be estimated via 'top-down' methods including eddy covariance flux towers which measure canopy-level gas exchange, or 'bottom-up' via measuring the individual components (Malhi 2012).

The GPP of tropical forests ranges from ~30 to 40 tonnes C per hectare per year and is demonstrably lower at dry or montane sites – these differences are directly attributable to the reduced growing season (Malhi 2012). A synthesis of data from 35 sites across the tropics revealed that allocation between canopy, fine root and woody NPP was relatively invariant and split roughly equally across the three components, though allocation to woody NPP was higher and roots lower in many of the Asian sites studied than in the American and Hawaiian sites (Malhi *et al.* 2011). Stem production was estimated to account for approximately 10 per cent of GPP, indicating that stem-based measures of growth may not be solely suitable proxies for carbon fluxes or their determinants (Malhi *et al.* 2011).

Climate, nutrients and perhaps region therefore have effect on both above-ground growth and productivity. The role of species composition in determining rates of production is not well understood, but functional traits may affect the efficiency of carbon acquisition. A study across Amazonia determined that the effect of environment on AGWP was much stronger than that of functional composition (Baker *et al.* 2009).

Tropical forests in global cycling of carbon

Plants take up atmospheric carbon as they grow and release it through respiration and senescence. Tropical forests store an estimated 460 billion tonnes of carbon in biomass and soil, comprising ~45 per cent of carbon in the terrestrial biosphere (Pan *et al.* 2011) and process 40 billion tonnes of carbon per year through GPP (Beer *et al.* 2010). Tropical forests are therefore critical to the global carbon cycle in terms of mopping up carbon from the atmosphere. Forests are also major sources of carbon to the atmosphere via deforestation and degradation and loss of forest cover reduces the ability for the terrestrial biosphere to further absorb carbon dioxide. An estimated 2 billion tonnes of carbon was released per year during the 1990s as a result of tropical deforestation, and approximately one third of human carbon dioxide emissions in the last decade have been from forest loss in the tropics (Malhi and Grace 2000; Richter and Houghton 2011). Rates of forest loss may also increase if incidence of fire and large-scale drought mortality interact with human-modified systems (Cochrane and Barber 2009; Aragão *et al.* 2014). There is, however, noted uncertainty and variability in estimates of CO_2 fluxes. Accurate estimation of both areal change in forest cover and carbon density (the amount of carbon stored in a given area) are needed to assess the contribution of landcover change in the tropics to global CO_2 emissions (Gibbs *et al.* 2007).

In addition to a real change in forest cover, the forests themselves are not in equilibrium. Data from large networks of forest inventory plots in Amazonia and Africa have, respectively, shown mean annual sinks of 0.45 (n plots = 123) and 0.63 tonnes C per hectare (n = 79) (Phillips *et al.* 2009; Lewis *et al.* 2009). There have been coincident changes in stem dynamics, showing higher rates of recruitment and mortality and increasing stand density (e.g. Phillips and Gentry 1994). The causes of these temporal trends have been hotly debated, but evidence suggests that they are at least partly attributable to increasing resource availability, such as CO_2 fertilization (Phillips and Lewis 2014). The shift to increasing biomass may, however, be transient and biomass may ultimately be limited by the constraints on canopy space, and eventually offset by increased rates of mortality (Malhi 2012). Since tropical forests can potentially be major sources or sinks of CO_2, there has been impetus to incorporate forest

management within policy directed at mitigating climate change. This has culminated in the development of Reduced Emissions from Deforestation and Degradation (REDD) policy (Miles and Kapos 2008). In essence, REDD provides economic incentives for countries, and particularly those in the developing world, to reduce deforestation rates and associated CO_2 emissions below a baseline (Miles and Kapos 2008). The extension, REDD+, additionally incorporates the role of sustainable management and enhancement of forest carbon stocks (Parker *et al.* 2009). Whilst simple in principle, a number of significant challenges must still be overcome before REDD+ policy can be successfully implemented, such as designating and distributing funds, setting baselines and ensuring permanence. Policies must also consider the needs of local populations and their need for sustainable development. Just as the nature of these forests, the ways in which they are used by humans and their threats vary between regions, so must strategies for their conservation.

Synthesis

Tropical forests are restricted to relatively warm and wet conditions, but strict definitions are numerous and this can be problematic for studying changes over space and time. Rather than a single, uniform entity, the tropical forest biome encompasses a great diversity of environments both in terms of climate and soil. Tropical forests have an equally rich and varied history, and the evolution of the angiosperm flora in isolated regions with different climatic and geological histories has led to unique species assemblages on different continents, and often even within regions. The diversity, structure and dynamics of these forests also vary greatly, although notably, when compared with other biomes, tropical forests store and cycle large amounts of carbon. Protection of tropical forests may provide a buffer to accelerated environmental change, but future climate change may challenge long-term persistence of tropical forest ecosystems.

Acknowledgements

References

Aragão, L. E. O. C., Poulter, B., Barlow, J. B., Anderson, L. O., Malhi, Y. and others (2014) 'Environmental change and the carbon balance of Amazonian forests', *Biological Reviews*, vol. 89, pp. 913–931.

Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L. and others (2004) 'Variation in wood density determines spatial patterns in Amazonian forest biomass', *Global Change Biology*, vol. 10, pp. 545–562.

Baker, T. R., Phillips, O. L., Laurance, W. F., Pitman, N. C. A., Almeida, S. and others (2009) 'Do species traits determine patterns of wood production in Amazonian forests?' *Biogeosciences*, vol. 6, pp. 297–307.

Banin, L., Feldpausch, T. R., Phillips, O. L., Baker, T. R., Lloyd, J. and others (2012) 'What controls tropical forest architecture? Testing environmental, structural and floristic drivers', *Global Ecology and Biogeography*, vol. 21, pp. 1179–1190.

Banin, L., Lewis, S. L., Lopez-Gonzalez, G., Baker, T. R., Quesada, C. A. and others (2014) 'Tropical forest wood production: a cross-continental comparison', *Journal of Ecology*, vol. 102, pp. 1025–1037.

Bartholomé, E. and Belward, A. S. (2005) GLC2000: a new approach to global land cover mapping from Earth observation data. International Journal of Remote Sensing, 26 (9): 1959–1977.

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M. and others (2010) 'Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate', *Science,* vol. 329, no. 5993, pp. 834–838.

Beckmann, G. G. (1983) 'Development of old landscapes and soils', in Division of Soils C (eds) *Soils: An Australian Viewpoint*, CSIRO, Melbourne, Australia.

Bradford, M. G., Murphy, H. T., Ford, A. J., Hogan, D. L., and Metcalfe, D. J. (2014) 'Long-term stem inventory data from tropical rain forest plots in Australia', *Ecology*, vol. 95, no 8, pp. 2362.

Bush, M. B., Silman, M. R. and Urrego, D. H. (2004) '48,000 years of climate and forest change in a biodiversity hot spot' *Science*, vol. 303, pp. 827–829.

Cannon, C. H., Morley, R. J., and Bush, A. B. G. (2009) 'The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance', *Proceedings of the National Academy of Sciences of the United States of America,* vol. 106, no. 27, pp. 11188–11193.

Chao, K. J., Phillips, O. L., Monteagudo, A., Torres-Lezama, A. and Martinez, R. V. (2009) 'How do trees die? Mode of death in northern Amazonia', *Journal of Vegetation Science*, vol. 20, pp. 260–268.

Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q. and others (2005) 'Tree allometry and improved estimation of carbon stocks and balance in tropical forests', *Oecologia*, vol. 145, pp. 87–99.

Chave, J., Condit, R., Muller-Landau, H. C., Thomas, S. C., Ashton, P. S. and others (2008) 'Assessing evidence for a pervasive alteration in tropical tree communities', *Plos Biology*, vol. 6, pp. 455–462.

Chave, J., Navarrete, D., Almeida, S., Alvarez, E., Aragão, L. and others (2010) 'Regional and seasonal patterns of litterfall in tropical South America', *Biogeosciences*, vol. 7, pp. 43–55.

Christensen, J. H., Krishna Kumar, K., Aldrian, E., An, S. –I., Cavalcanti, I. F. A. and others (2013) 'Climate Phenomena and their Relevance for Future Regional Climate Change' in T. F. Stocker, D. Qin, G. –K. Plattner, M. Tignor, S. . Allen, J. and others (eds.) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, UK.

Churkina, G. and Running, S. W. (1998) 'Contrasting climatic controls on the estimated productivity of global terrestrial biomes', *Ecosystems*, vol. 1, pp. 206–215.

Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R. and others (2001) 'Net primary production in tropical forests: An evaluation and synthesis of existing field data', *Ecological Applications*, vol. 11, pp. 371–384.

Cochrane, M. A. and Barber, C. P. (2009) 'Climate change, human land use and future fires in the Amazon', *Global Change Biology*, vol. 15, pp. 601–612.

Corlett, R. T. (2007) 'What's so special about Asian tropical forests?', *Current Science*, 93, 1551–1557.

Corlett, R. T. (2011) 'Impacts of warming on tropical lowland rainforests', *Trends in Ecology and Evolution,* vol. 26, no 11, pp. 606–613.

Cox, C. B. and Moore, P. D. (2000) *Biogeography: An Ecological and Evolutionary Approach,* Sixth Edition, Blackwell Science Ltd, Oxford, UK.

Del Grosso, S. (2008) 'Global potential net primary production predicted from vegetation class, precipitation, and temperature', *Ecology*, vol. 89, pp. 2971–2971.

Donoghue, M. J. (2008) 'A phylogenetic perspective on the distribution of plant diversity', *Proceedings of the National Academy of Sciences of the United States of America*, vol. 105, pp. 11549–11555.

Dudal, R. (2005) 'Soils of Southeast Asia' in A. Gupta (ed.) *The Physical Geography of Southeast Asia,* Oxford University Press, Oxford, UK.

FAO [Food and Agriculture Organization of the United Nations] (2008) Harmonized world soil database, version 1.0. FAO Land and Water Digital Media Series 34. FAO/IIASA/ISRIC/JRC-EU/Academia Sinica, Rome, Italy. www.fao.org/nr/land/soils/harmonized-world-soil-database/en

Fauset, S., Baker, T. R., Lewis, S. L., Feldpausch, T. R., Affum-Baffoe, K. and others (2012) 'Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana', Ecology Letters, vol. 15, pp. 1120–1129.

Feeley, K. J., Davies, S. J., Perez, R., Hubbell, S. P. and Foster, R. B. (2011) 'Directional changes in the species composition of a tropical forest', *Ecology*, vol. 92, pp. 871–882.

Feldpausch, T. R., Banin, L., Phillips, O. L., Baker, T. R., Lewis, S. L. and others (2011) 'Height-diameter allometry of tropical forest trees', *Biogeosciences*, vol. 8, pp. 1081–1106.

Gibbs, H. K., Brown, S., Niles, J. O. and Foley, J. A. (2007) 'Monitoring and estimating tropical forest carbon stocks: making REDD a reality', *Environmental Research Letters*, vol. 2, no 4, 045023.

AQ: Please check

Giresse, P., Maley, J. and Brenac, P. (1994) 'Late quaternary paleoenvironments in the Lake Barombi Mbo (West Cameroon) deduced from pollen and carbon isotopes of organic-matter', *Palaeogeography Palaeoclimatology Palaeoecology*, vol. 107, pp. 65–78.

Gentry, A. H. (1988) 'Changes in plant community diversity and floristic composition on environmental and geographical gradients', *Annals of the Missouri Botanical Garden*, vol. 75, pp. 1–34.

Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G. and Wright, S. J. (2003) 'Cloud cover limits net CO2 uptake and growth of a rainforest tree during tropical rainy seasons', *Proceedings of the National Academy of Sciences of the United States of America*, vol. 100, pp. 572–576.

Guilderson, T. P., Fairbanks, R. G. and Rubenstone, J. L. (1994) 'Tropical Temperature-Variations since 20,000 Years Ago – Modulating Interhemispheric Climate-Change', *Science*, vol. 263, pp. 663–665.

Hammond, D. S. (2005) 'Biophysical Features of the Guiana Shield' in D. S. Hammond (ed.) *Tropical Forests of the Guiana Shield*, CABI Publishing, Wallingford, Oxfordshire., UK

Hawkins, E., Joshi, M., and Frame, D. (2014) 'Wetter then drier in some tropical areas', *Nature Climate Change*, vol. 4, no 8, pp. 646–647.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A. (2005) 'Very high resolution interpolated climate surfaces for global land areas', *International Journal of Climatology*, vol. 25, pp. 1965–1978.

Holdridge, L. R. (1947) 'Determination of world plant formations from simple climatic data', *Science*, vol. 105, pp. 367–368.

Hubble, G. D. and Isbell, R. F. (1983) 'Eastern Highlands (VI)', in Division of Soils C (eds) *Soils: An Australian Viewpoint*, CSIRO, Melbourne, Australia.

Hubble, G. D., Isbell, R. F. and Northcote, K. H. (1983) 'Features of Australian soils', in Division of Soils C (eds) *Soils: An Australian Viewpoint*, CSIRO, Melbourne, Australia.

Huston, M. A. (2012) 'Precipitation, soils, NPP, and biodiversity: resurrection of Albrecht's curve', *Ecological Monographs*, vol. 82, no 3, pp. 277–296.

Irion, G. (1978) 'Soil infertility in Amazonian rain-forest', *Naturwissenschaften*, vol. 65, pp. 515–519.

IUSS Working Group WRB (2006) 'World reference base for soil resources', in *World Soil Resources Reports No. 103*, FAO Rome.

Jenny, H. (1941) *Factors of Soil Formation: A System of Quantitative Pedology*. McGraw-Hill, New York.

Jordan, C. F. and Herrera, R. (1981) 'Tropical rain forests – are nutrients really critical', *American Naturalist*, vol. 117, pp. 167–180.

Juo, A. S. R. and Wilding, L. P. (1996) 'Soils of the lowland forests of West and Central Africa', *Proceedings of the Royal Society of Edinburgh Section B (Biological Sciences)*, vol. 104, pp. 15–29.

Kaspari, M., Garcia, M. N., Harms, K. E., Santana, M., Wright, S. J. and Yavitt, J. B. (2008) 'Multiple nutrients limit litterfall and decomposition in a tropical forest', *Ecology Letters*, vol. 11, pp. 35–43.

Keeling H. C. and Phillips O. L. (2007) 'The global relationship between forest productivity and biomass'. *Global Ecology and Biogeography*, 16, 618–631.

Kellman, M. and Tackaberry, R. (1997) *Tropical Environments: The Functioning and Management of Tropical Ecosystems*, Routledge, London.

Kitayama, K. and Aiba, S. I. (2002) 'Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo', *Journal of Ecology*, vol. 90, pp. 37–51.

Kho, L. K., Malhi, Y., and Tan, S. K. S. (2013) 'Annual budget and seasonal variation of aboveground and belowground net primary productivity in a lowland dipterocarp forest in Borneo', *Journal of Geophysical Research: Biogeosciences*, vol. 118, no 3, pp. 1282–1296.

Köppen, W. (1923) *Die climate de erde: grundiss der klimakunde*. De Greyte, Berlin.

LaFrankie, J. V., Ashton, P. S., Chuyong, G. B., Co, L., Condit, R. and others (2006) 'Contrasting structure and composition of the understory in species-rich tropical rain forests', *Ecology*, vol. 87, pp. 2298–2305.

Laurance, W. F., Fearnside, P. M., Laurance, S. G., Delamonica, P., Lovejoy, T. E. and others (1999) 'Relationship between soils and Amazon forest biomass: A landscape-scale study', *Forest Ecology and Management*, vol. 118, pp. 127–138.

Lewis, S. L., Lopez-Gonzalez, G., Sonke, B., Affum-Baffoe, K., Baker, T. R. and others (2009) 'Increasing carbon storage in intact African tropical forests', *Nature*, vol. 457, pp. 1003-U3.

Lewis, S. L., Sonké, B., Sunderland, T., Begne, S. K., Lopez-Gonzalez, G. and others (2013) 'Above-ground biomass and structure of 260 African tropical forests', *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 368, 20120295.

Li, J., Xie, S. P., Cook, E. R., Huang, G., D'Arrigo, R. and others (2011) 'Interdecadal modulation of El Niño amplitude during the past millennium', *Nature Climate Change*, vol. 1, no 2, pp. 114–118.

Lidgard, S. and Crane, P. R. (1988) 'Quantitative-analyses of the early angiosperm radiation', *Nature*, vol. 331, pp. 344–346.

Lloyd, J. and Farquhar, G. D. (2008) 'Effects of rising temperatures and CO_2 on the physiology of tropical forest trees', *Philosophical Transactions of the Royal Society B-Biological Sciences*, vol. 363, 1811–1817.

Losos, E. and Leigh, E. G. (2004) *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*, University of Chicago Press, Chicago, USA.

Luyssaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichsteins, M. and others (2007) 'CO_2 balance of boreal, temperate, and tropical forests derived from a global database', *Global Change Biology*, vol. 13, pp. 2509–2537.

Malhi, Y. (2012) 'The productivity, metabolism and carbon cycle of tropical forest vegetation', *Journal of Ecology*, vol. 100, no 1, pp. 65–75.

Malhi, Y. and Grace, J. (2000) 'Tropical forests and atmospheric carbon dioxide', *Trends in Ecology and Evolution*, vol. 15, pp. 332–337.

Malhi, Y. and Wright, J. (2004) 'Spatial patterns and recent trends in the climate of tropical rainforest regions', *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, vol. 359, pp. 311–329.

Malhi, Y., Baker, T. R., Phillips, O. L., Almeida, S., Alvarez, E. and others (2004) 'The above-ground coarse wood productivity of 104 Neotropical forest plots', *Global Change Biology*, vol. 10, pp. 563–591.

Malhi, Y., Wood, D., Baker, T. R., Wright, J., Phillips, O. L. and others (2006) 'The regional variation of aboveground live biomass in old-growth Amazonian forests', *Global Change Biology*, vol. 12, pp. 1107–1138.

Malhi, Y., Aragão, L. E., Galbraith, D., Huntingford, C., Fisher, R. and others (2009) 'Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest', *Proceedings of the National Academy of Sciences*, vol. 106, no 49, 20610–20615.

Malhi, Y., Doughty, C. And Galbraith, D. (2011) 'The allocation of ecosystem net primary productivity in tropical forests', *Philosophical Transactions of the Royal Society B,* vol. 366, pp. 3225–3245.

Mayaux, P., Holmgren, P., Achard, F., Eva, H., Stibig, H. and Branthomme, A. (2005) 'Tropical forest cover change in the 1990s and options for future monitoring', *Philosophical Transactions of the Royal Society B-Biological Sciences*, vol. 360, pp. 373–384.

McGregor, G. R. and Nieuwolt, S. (1998) *Tropical Climatology: An Introduction to the Climates of the Low Latitudes*, Second edition, John Wiley and Sons, Chichester, UK.

McGroddy, M. E., Daufresne, T. and Hedin, L. O. (2004) 'Scaling of C:N:P: stoichiometry in forest ecosystems worldwide: implications of terrestrial Redfield-type ratios', *Ecology,* vol. 85, pp. 2390–2401.

McMahon, T. (1973) 'Size and Shape in Biology', *Science*, vol. 179, pp. 1201–1204.

Miles, L. and Kapos, V. (2008) 'Reducing greenhouse gas emissions from deforestation and forest degradation: Global land-use implications', *Science*, vol. 320, pp. 1454–1455.

Mirmanto, E., Proctor, J., Green, J., Nagy, L. and Suriantata (1999) 'Effects of nitrogen and phosphorus fertilization in a lowland evergreen rainforest', *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, vol. 354, pp. 1825–1829.

Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C. and others (2003) 'Climate-driven increases in global terrestrial net primary production from 1982 to 1999', *Science*, vol. 300, pp. 1560–1563.

New, M., Hulme, M. and Jones, P. (1999) 'Representing twentieth-century space–time climate variability. Part I: Development of a 1961–90 mean monthly terrestrial climatology', *Journal of Climate*, vol. 12, pp. 829–856.

Pan, Y., Birdsey, R., Fang, J., Houghton, R., Kauppi, P. and others (2011) 'A large and persistent carbon sink in the world's forests', *Science,* vol. 333, pp. 988–992.

Paoli, G. D. and Curran, L. M. (2007) 'Soil nutrients limit fine litter production and tree growth in mature lowland forest of Southwestern Borneo', *Ecosystems*, vol. 10, pp. 503–518.

Parker, C., Mitchell, A., Trivedi, M., Mardas, N. and Sosis, K. (2009) *The Little REDD+ Book,* Global Canopy Programme, Oxford, UK.

Peacock, J., Baker, T. R., Lewis, S. L., Lopez-Gonzalez, G. and Phillips, O. L. (2007) 'The RAINFOR database: monitoring forest biomass and dynamics', *Journal of Vegetation Science*, vol. 18, pp. 535–542.

Phillips, O. L. and Gentry, A. H. (1994) 'Increasing turnover through time in tropical forests', *Science*, vol. 263, pp. 954–958.

Phillips, O. L. and Lewis, S. L. (2014) 'Evaluating the tropical forest carbon sink', *Global Change Biology*, vol. 20, 2039–2041.

Phillips, O. L., Aragão, L., Lewis, S. L., Fisher, J. B., Lloyd, J. and others (2009) 'Drought sensitivity of the Amazon rainforest', *Science*, vol. 323, pp. 1344–1347.

Phillips, O. L., van der Heijden, G., Lewis, S. L., López-González, G., Aragão, L. E. O. C. and others (2010) 'Drought–mortality relationships for tropical forests', *New Phytologist*, vol. 187, pp. 631–646.

Primack, R. B. and Corlett, M. T. (2005) *Tropical Rainforests: An Ecological and Biogeographical Comparison,* Blackwell Publishing, Oxford, UK.

Putz, F. E. and Redford, K. H. (2010) 'The importance of defining 'forest': tropical forest degradation, deforestation, long-term phase shifts, and further transitions', *Biotropica*, vol. 42, pp. 10–20.

Quesada, C.A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T.R. and others (2012a) 'Variations in chemical and physical properties of Amazon forest soils in relation to their genesis', *Biogeosciences*, vol. 7, pp. 1515–1541.

Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R. and others (2012b) 'Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate', *Biogeosciences*, vol. 9, pp. 2203–2246.

Richter, D. de B. and Houghton, R. A.: Gross CO2 fluxes from landuse change: Implications for reducing global emissions and increasing sinks, *Carbon Management*, 2, 41–47, 2011.

Ryan, M. G. and Yoder, B. J. (1997) 'Hydraulic limits to tree height and tree growth', *Bioscience*, vol. 47, pp. 235–242.

Saatchi, S., Houghton, R.A., Dos Santos Alvala, R.C., Soares, J.V. and Yu, Y. (2007) 'Distribution of aboveground live biomass in the Amazon basin', *Global Change Biology*, vol. 13, pp. 819–837.

Schuur, E. A. G. (2003) 'Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation', *Ecology*, vol. 84, pp. 1165–1170.

Shuttleworth, W. J. (1988) 'Evaporation from Amazonian rainforest', *Proceedings of the Royal Society of London Series B Biological Sciences*, vol. 233, pp. 321–346.

Slik, J. W. F., Paoli, G., McGuire, K., Amaral, I., Barroso, J. and others (2013) 'Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics', *Global Ecology and Biogeography*, vol. 22, pp.1261–1271.

Stephenson, N. L., van Mantgem, P. J., Bunn, A. G., Bruner, H., Harmon, M. E. and others (2011) 'Causes and implications of the correlation between forest productivity and tree mortality rates', *Ecological Monographs*, vol. 81, pp. 527–555.

Stark, N. M. and Jordan, C. F. (1978) 'Nutrient Retention by Root Mat of an Amazonian Rain-Forest', *Ecology*, vol. 59, pp. 434–437.

Torello-Raventos, M., Feldpausch, T. R., Veenendaal, E., Schrodt, F., Saiz, G. and others (2013) 'On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions', *Plant Ecology and Diversity,* vol. 6, pp. 101–137.

Townsend, A. R., Asner, G. P. and Cleveland, C. C. (2008) 'The biogeochemical heterogeneity of tropical forests', *Trends in Ecology and Evolution*, vol. 23, pp. 424–431.

Vitousek, P. M. (1984) 'Litterfall, nutrient cycling, and nutrient limitation in tropical forests', *Ecology*, vol. 65, pp. 285–298.

Walsh, R. P. D. (1996a) 'Climate', in P. W. Richards (ed.) *The Tropical Rain Forest: An Ecological Study*, Cambridge University Press, Cambridge, UK.

Walsh, R. P. D. (1996b) 'Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics', *Journal of Tropical Ecology*, vol. 12, pp. 385–407.

Whittaker, R. H. (1975) *Communities and Ecosystems,* 2nd edition, McMillan, New York.

Williams, J. W., Jackson, S. T. and Kutzbach, J. E. (2007) 'Projected distributions of novel and disappearing climates by 2100 AD', *Proceedings of the National Academy of Sciences of the United States of America*, vol. 104, no 14, pp. 5738–5742.

Woodward, F. I., Lomas, M. R. and Kelly, C. K. (2004) 'Global climate and the distribution of plant biomes', *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, vol. 359, pp. 1465–1476.

Wright, S. J., Muller-Landau, H. C. and Schipper, J. (2009) 'The future of tropical species on a warmer planet', *Conservation Biology*, vol. 23, pp. 1418–1426.

Wright, S. J., Yavitt, J. B., Wurzburger, N., Turner, B. L., Tanner, E. V. J. and others (2011) 'Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest', *Ecology*, vol. 92 pp.1616–1625.

Zelazowski, P., Malhi, Y., Huntingford, C., Sitch, S. and Fisher, J. B. (2011) 'Changes in the potential distribution of humid tropical forests on a warmer planet', *Philosophical Transactions of the Royal Society A*, vol. 369, pp. 137–160.