Chapter 2

Understanding tropical forests

Think of a 'tropical forest' and images of equatorial rain forest probably spring to mind — evergreen forest, teaming with wildlife and drenched in rain — but many other forest types grow in the tropics. In seasonally dry climates, evergreen forest types in wetter areas alternate abruptly with deciduous forest types in drier sites, grading into grassy savannahs in the driest areas. Likewise, on mountains, forest structure changes dramatically with elevation. In more limiting environments, there are swampy peat forests, salty mangrove forests and acidic heath forests. Different forest types function differently, and each has distinctive characteristics that present restoration projects with different challenges. In evergreen forests, the major challenge is ensuring the rapid recovery of the high levels of biodiversity that characterize such ecosystems; whereas in drier forests simply getting planted trees to survive the first dry season is a major achievement. The climax forest type defines the goal of restoration (i.e. the 'target' see Section 1.2), so it is important to know which forest type you are dealing with.

2.1 Tropical forest types

Many different schemes to classify tropical forest types have been proposed. These are based on various criteria including climate, soil, species composition, structure, function and successional stage (Montagnini & Jordan, 2005). Commonly used schemes include Whitmore's system (1998) **Box 2.1**, which is based on climate and elevation, and UNEP–WCMC's forest category classification (UNEP–WCMC, 2000), which also includes disturbed forests and plantations (see **Box 2.2**).

Evergreen tropical forests (including rain forests)

Tropical rain forests are the most highly developed of evergreen tropical forests. They mostly grow within 7° latitude from the equator, where mean annual temperatures exceed 23°C and mean monthly temperatures are higher than 18°C (i.e. there is no frost). Annual rainfall exceeds 4,000 mm, with monthly rainfall averaging more than 100 mm all year round (i.e. there is no significant dry season). Other types of evergreen tropical forest grow wherever rainfall exceeds evapotranspiration (usually where mean annual rainfall is more than 2,000 mm) and the dry season is no longer than 2 months. They extend up to 10° latitude from the equator. The greatest expanses of evergreen tropical forests are in the lowland Amazon Basin, the Congo Basin, the Malay Peninsula, and the Southeast Asian islands of Indonesia and New Guinea.
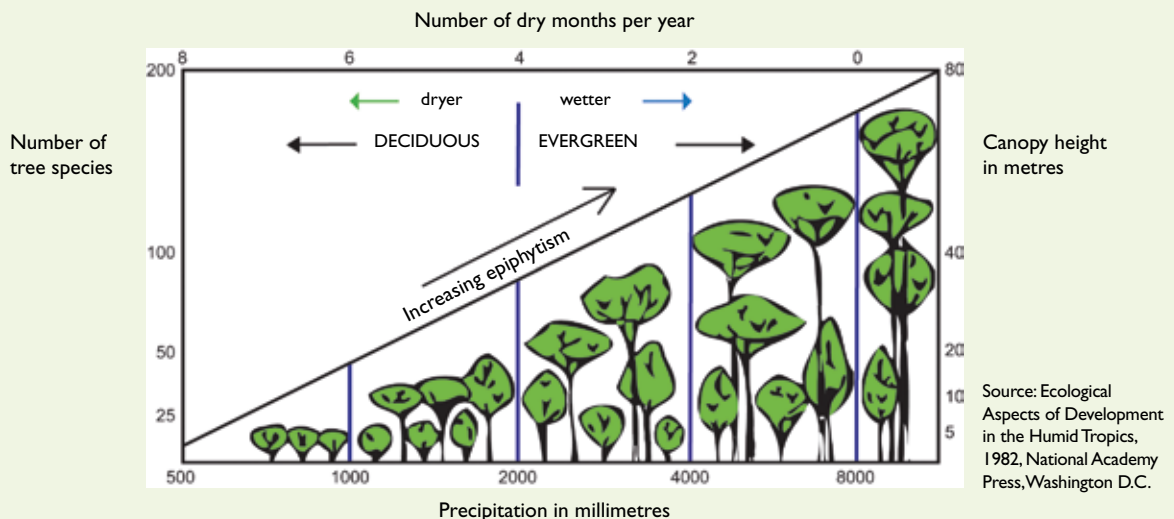
Tropical rain forest at Maliau Basin Conservation Area, Sabah, East Malaysia

Box 2.1. Whitmore's simple classification of tropical forest types.

Whitmore's (1998) simple classification of tropical forest types proposes that on moving away from the equator, climax tropical forests can be broadly grouped into two main categories: seasonally dry and everwet. Superimposed upon the effects of latitude and the prevailing climate are the effects of elevation (i.e. montane or lowland forests) and substrate (e.g. forests growing on limestone or peat etc.).

Climate	Elevation	Tropical forest types
Seasonally dry		Monsoon (deciduous) forests of various types Semi-evergreen rain forest
Everwet	Lowlands	Lowland evergreen rain forest
	Montane 1,200–1,500 m	Lower montane rain forest
	Montane 1,500–3,000 m	Upper montane rain forest or cloud forest
	Montane > 3,000 m	Subalpine forest to climatic tree limit
	Usually lowland	Heath forest Limestone forest Ultrabasic forest Mangrove forest Peat swamp forest Freshwater swamp forest Freshwater periodic swamp forest

Number of dry months per year

Source: Ecological Aspects of Development in the Humid Tropics, 1982, National Academy Press, Washington D.C.

The relationship between moisture and plant life in a tropical lowland forest. The diagonal line from left to right represents a gradient of mean annual precipitation, demonstrating that as the amount of moisture increases, forests become more complex, with greater biological diversity and ecological stratification. (Source: Assembly of Life Sciences (U.S.A.), 1982.)

Box 2.2. UNEP–WCMC's forest category classification.

UNEP–WCMC's forest category classification, developed in 1990, divides the world's forests into 26 major types (on the basis of climate zone and characteristic tree species) of which the 15 listed below are tropical (UNEP–WCMC, 2000). For each tropical forest type, The International Tropical Timber Organization (ITTO) proposes another layer of classification, based on successional stage, i.e. primary, managed primary, modified natural, degraded, secondary or planted.
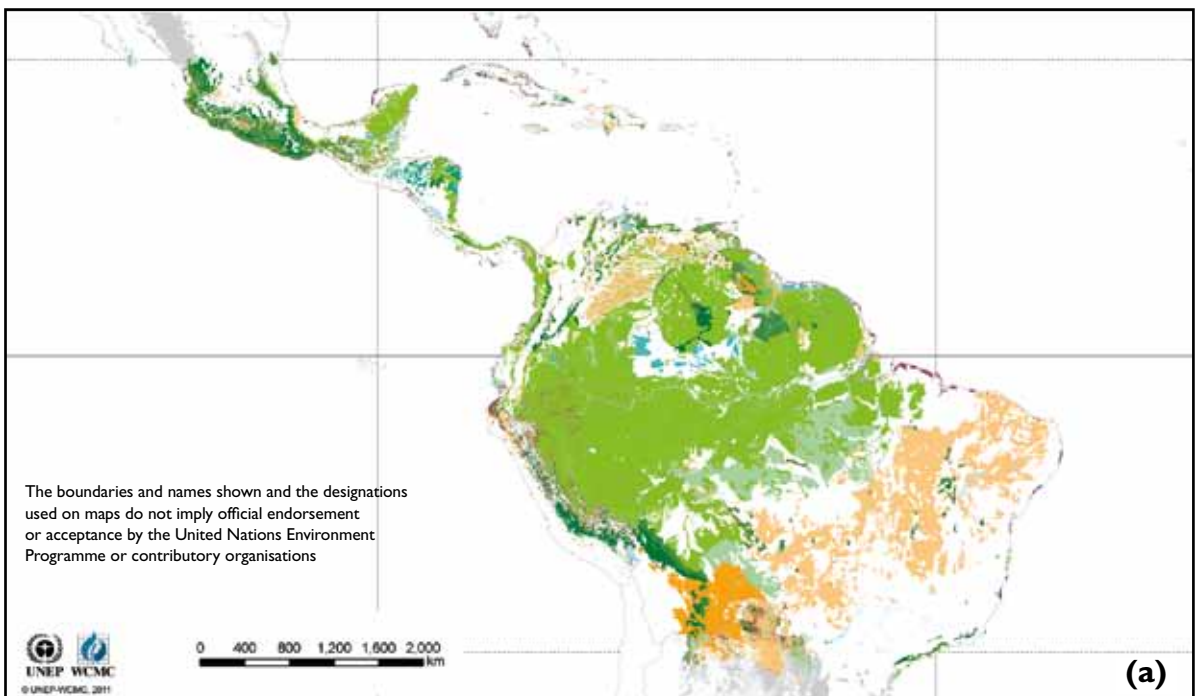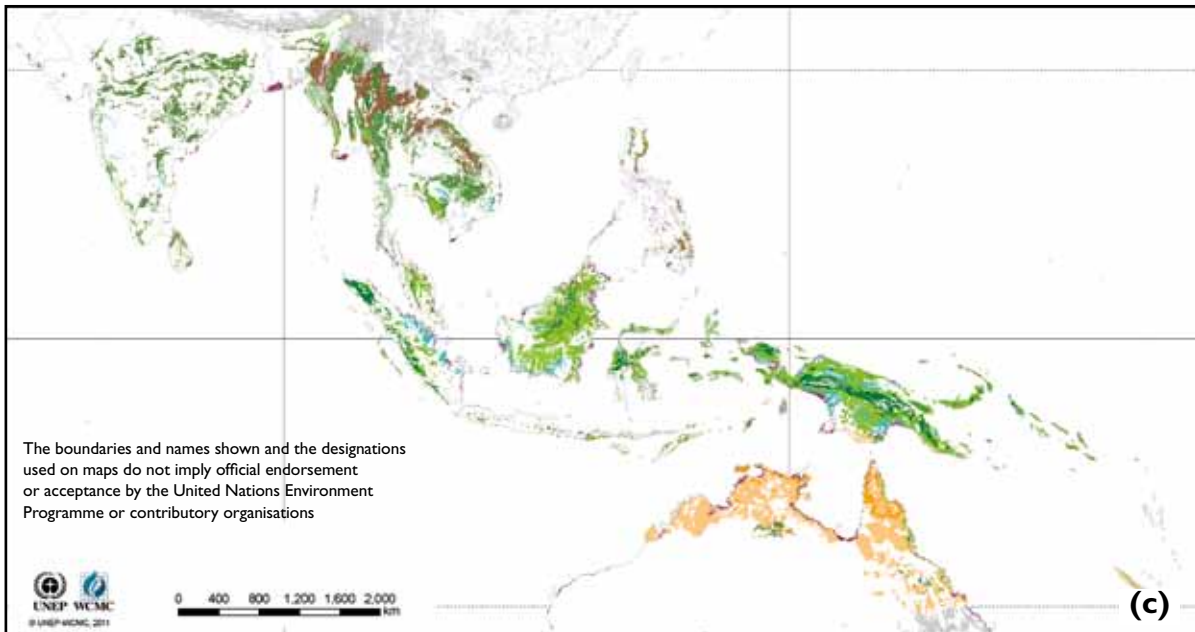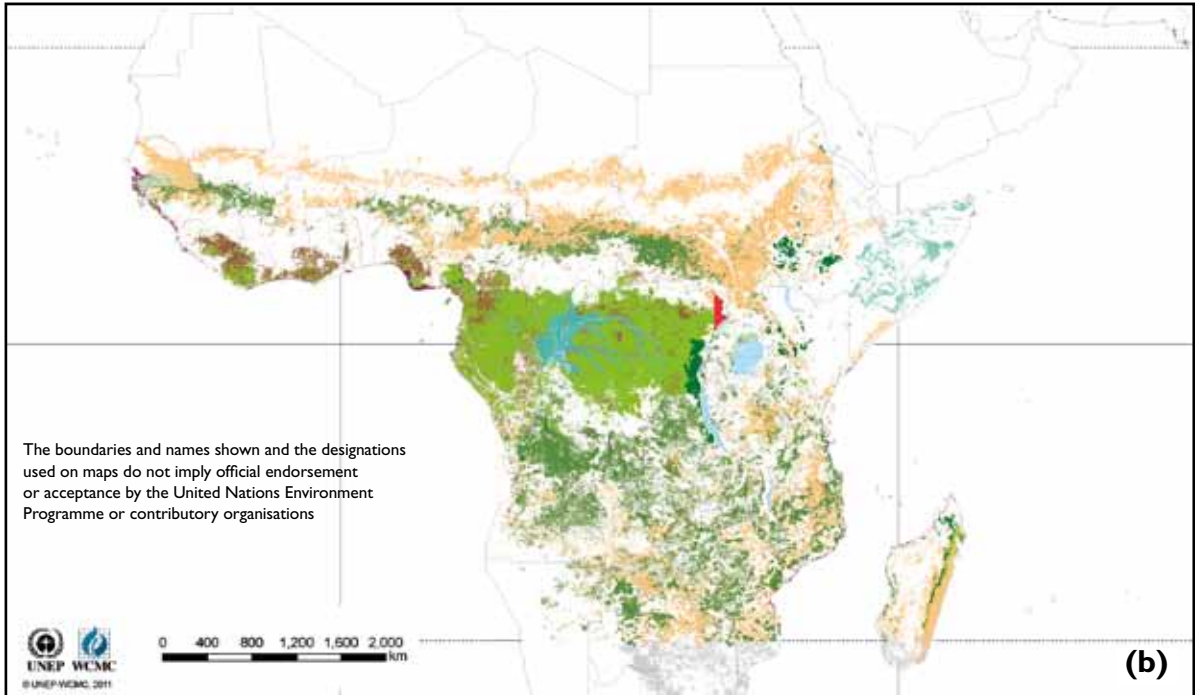
TROPICAL FOREST TYPES

- Mangrove
- Freshwater swamp forest
- Upper montane forest
- Lowland evergreen broadleaf rainforest
- Lower montane forest
- Semi-evergreen moist broadleaf forest
- Exotic species plantations
- Native species plantations
- Mixed needleleaf/broadleaf forest

- Needleleaf forest
- Sclerophyllous dry forest
- Deciduous/semi-deciduous broadleaf forest
- Thorn forest
- Sparse trees/parkland
- Disturbed natural forest

OTHER TYPES

- Temperate and boreal forests
- Water bodies
- No data

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0 400 800 1,200 1,600 2,000 km

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Extent of major tropical forest types of a) Central/South America b) Africa and c) Asia, based on UNEP–WCMC's classification of 1990, derived from a number of different national and international sources. The scales and dates vary between sources, and this synthesis can be considered to show global cover in approximately 1995. The forest classification was designed to reflect the characteristics of forests that are relevant to conservation and to facilitate harmonisation between various national and international classification systems. © UNEP–WCMC, 2011.

Evergreen tropical forests are the most luxuriant of all tropical forests, with structural complexity and biodiversity that usually exceed those of other tropical forest types, although there is immense variability. In sample plots in Ecuador, for example, Whitmore (1998) cited extremes of 370 tree species per hectare, compared with just 23 tree species per hectare at a Nigerian site. At least five canopy strata can usually be distinguished (i.e. ground flora, shrubs (including tree saplings), understory trees, main canopy trees and emergent trees), with the main canopy occurring up to 45 m above the ground and some emergent trees soaring up to 60 m. Most light is captured by the main canopy,

Buttresses are a characteristic feature of many evergreen tropical forest tree species. The Waorani Indians make use of them for communication. The low frequency boom, produced when the buttresses are thumped carries over considerable distances.
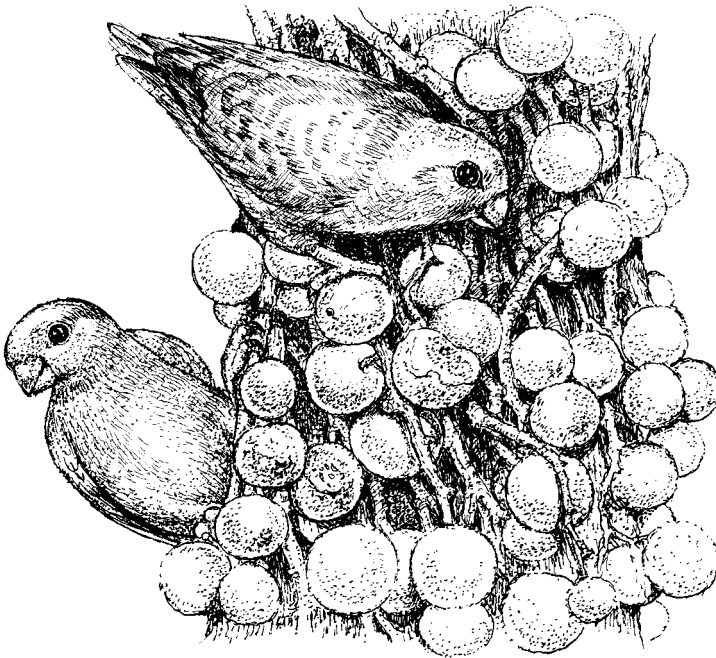
so the shade-tolerant ground and shrub layers tend to be less dense than those in drier tropical forests. Buttressed trees are common, particularly on shallow soils. Cauliflory (i.e. the growth of flowers and fruits on tree trunks) is also characteristic, particularly for understory trees, whose leaves also tend to have 'drip tips' (i.e. elongated acumen) that allow them to shed water rapidly. Some canopy trees may be briefly deciduous, but the canopy as a whole is evergreen. Woody climbers (including rattans in Asia and Africa), fig trees (*Ficus* spp.) and dense communities of epiphytic ferns and orchids (along with bromeliads in South America and Apocynaceae and Rubiaceae species in Asia) are also characteristic of tropical rain forests.

Theobroma cacao pods are an example of a cauliflorus fruit.

Most food resources provided by evergreen forests (i.e. leaves, fruits, insects etc.) are in the canopy, so most of the animals live there and provide the trees with services vital for reproduction. The most important pollinators are bees and wasps, but nectar-eating birds and bats also pollinate many tree species. Seed dispersal is mostly carried out by frugivorous birds, along with fruit bats and primates and, when fruit falls to the ground, ungulates and rodents. Seed dispersal by wind is rare except for the tallest trees (the Dipterocarps of tropical Asia being an obvious exception). The heavy dependence of evergreen tropical forest trees on animals for reproduction is critical when considering forest restoration.
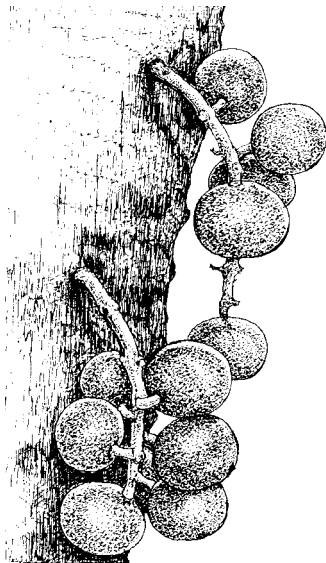
Double-eyed fig parrots feast on figs and disperse their seeds. This crucial ecological service is vital to the forest's survival and encouragement of it is essential for successful forest restoration.

Buttressed tree in a lowland evergreen forest, Cameroon. (Photo: A. McRobb)

Many tree species in evergreen tropical forests (like this *Baccaurea ramiflora* from Southeast Asia) produce flowers and fruits directly from trunks or branches. The flowers are more visible to pollinators and the fruits to seed dispersers as they are not hidden by foliage.

In evergreen tropical forests, the leaves of many tree species have elongated acumen or 'drip tips' which help them to shed rain water more efficiently, thereby preventing the smothering growth of mosses and lichens on the leaf surface.
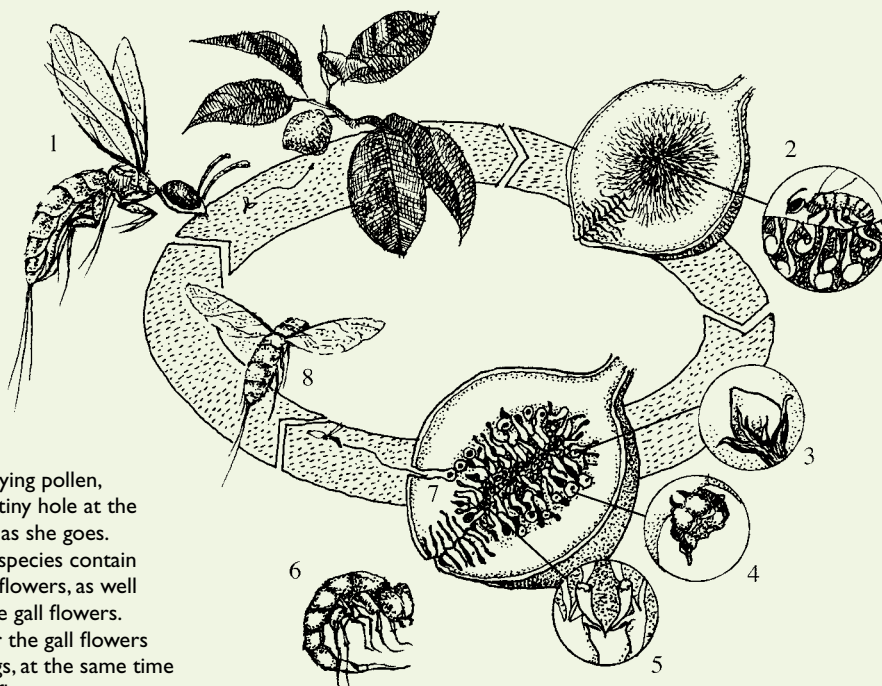
Box 2.3. The essential nature of fig trees (*Ficus* spp.).

Fig trees are keystone species in tropical forest ecosystems, so restoration projects should always include them. The pantropical genus *Ficus* comprises more than 1,000 species of vines, woody climbers, shrubs and large trees and it is their unique reproductive mechanism that makes them keystone species. Sometimes mistaken for fruit, the parts of the fig tree that are eaten (called 'syconia' in botanical language) often grow on short stalks on the trunk or large branches and are a vital food for forest animals. Syconia are actually the swollen stalks of inflorescences (receptacles), which have become inverted to enclose many tiny flowers or fruits inside.

The flowers of each *Ficus* species are pollinated by one (or very few) fig wasp species. Figs provide the only means for wasp reproduction, and the wasps are the only way that fig flowers can be pollinated. Fig wasps complete their life-cycle in just a few weeks so, somewhere in the forest, figs of all species must be available all year round so that the wasps do not die out, leaving the fig trees unable to reproduce. The loss of *Ficus* species from a tropical forest is disastrous because it causes arboreal birds and mammals that rely on figs in times of food shortage to die out gradually. Much later, the tree species that rely on these animals for seed dispersal are also lost.

Planting fig trees restores ecological balance by attracting seed-dispersing animals into restoration plots. In addition, fig trees grow very dense root systems, which enable them to grow well under the harshest conditions and to grow back rapidly after burning or slashing. *Ficus* species are therefore excellent for preventing soil erosion and stabilising river banks.

The life cycle of fig wasps.

1. A female fig wasp, carrying pollen, enters a fig through a tiny hole at the apex, losing her wings as she goes.
2. The figs of some *Ficus* species contain both male and female flowers, as well as short-styled infertile gall flowers. The wasp searches for the gall flowers in which to lay her eggs, at the same time pollinating the female flowers.
3. Wasp larvae develop in the gall flowers. Pollinated female flowers develop into fruits.
4. Wingless male wasps emerge from their gall nurseries first. They mate with female wasps shortly before the females emerge from their galls.
5. By the time the females emerge, the male flowers are producing pollen.
6. The males chew a hole through the wall of the fig.
7. Females escape through the hole, collecting pollen as they go.
8. Female wasps, laden with pollen, then fly to another fig tree and the cycle continues.

Challenges to restoring evergreen tropical forests

Achieving high biodiversity and structural complexity is the greatest challenge when restoring evergreen tropical forests. Recovery of full biodiversity is difficult to achieve when so many species are involved in such complex ecological relationships, especially because the ecology, reproductive biology and propagation of most tropical tree species are poorly understood.

Selectively logged forests, or even some clear-cut sites that have not been disturbed further, may respond well to accelerated natural regeneration (ANR; see **Section 5.2**); whereas tree planting is usually necessary in degraded sites that are dominated by grasses and herbs. The great richness of tree species in evergreen tropical forests presents a huge choice from which to select high-performing trees for planting. Focusing first on the small minority of deciduous tree species that grow in evergreen forests can often achieve rapid results because such species resist desiccation in exposed, dry, deforested sites by shedding their leaves during the driest months of the year.

One consequence of tree species richness is that trees of the same species are usually spaced far apart from each other. This makes it difficult to locate enough seed trees to ensure high genetic diversity amongst trees grown in nurseries. Furthermore, fruiting can be irregular and many tree species have recalcitrant seeds that cannot be stored easily. Many evergreen forest tree species have large seeds that can only be dispersed by large animals, many of which (rhinos, elephants, tapirs etc.) have been extirpated from large parts of their former ranges. Therefore, including large-seeded tree species amongst those chosen for planting can help to conserve them (Vanthomme *et al*., 2010). Even small-seeded tree species are mostly dispersed by birds, bats and small mammals, so preventing the hunting of such animals is vital to enable the recruitment of non-planted tree species into planted sites.

Year-round, abundant water, warmth and light in the wet tropics mean that trees can be planted at any time of the year, and getting them to survive and grow well is less of a problem than in drier regions. However, these conditions are also optimal for weed growth, so frequent weeding is necessary and weeding costs may be high. Fire is usually less of a problem than in drier areas, but it is more likely in degraded forest and climate change will exacerbate the problem. Hence, fire-prevention measures may still be necessary.
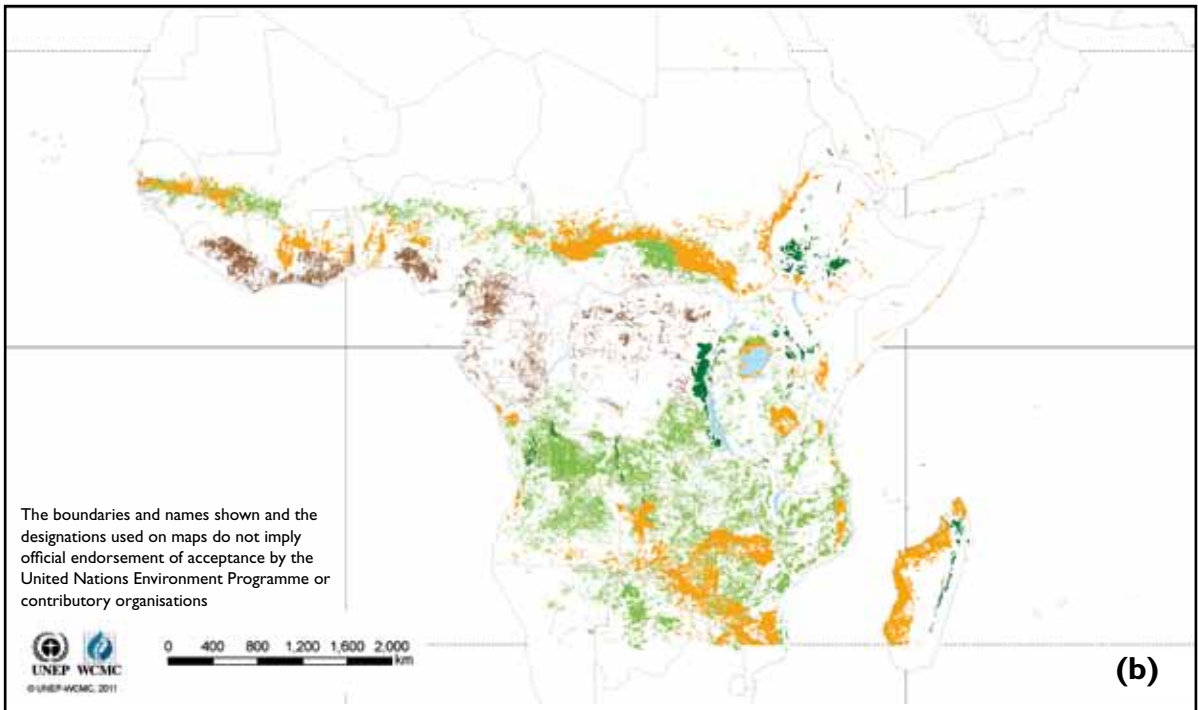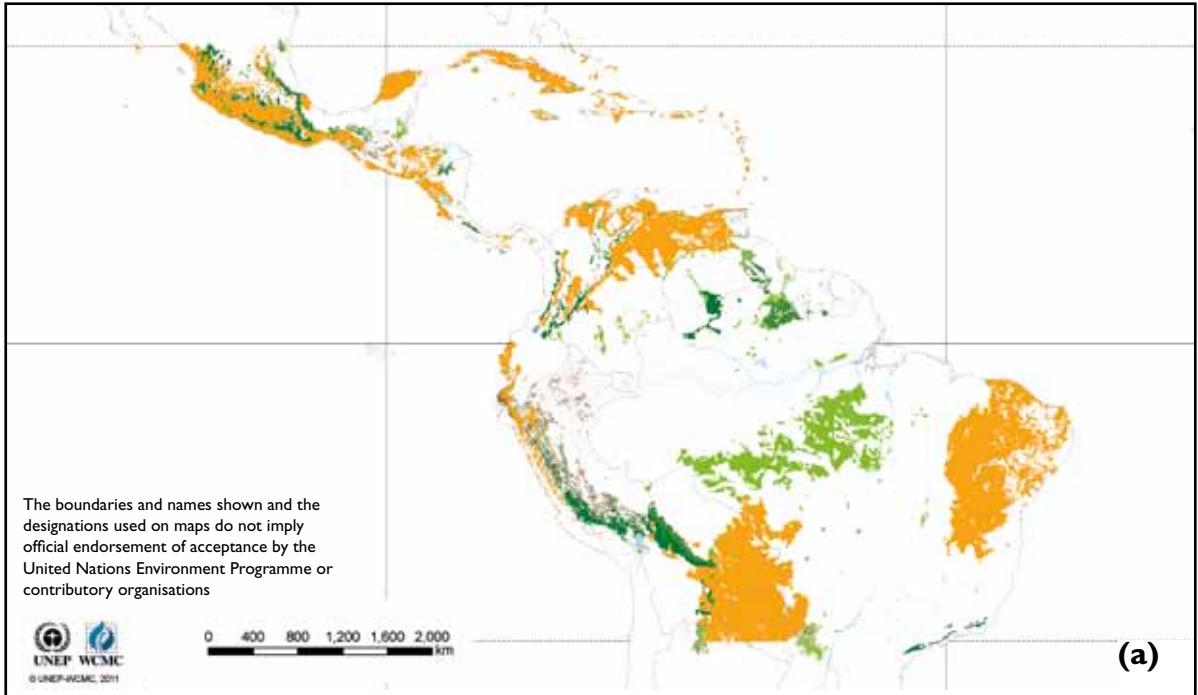
Seasonal tropical forests

Seasonally dry tropical forests or 'monsoon' forests are most prevalent at 5–15° latitude from the equator, where rainfall and day length vary annually. Such forests grow where annual rainfall averages 1,000–2,000 mm and there is a short cool season. During the longer dry season (3–6 months), many trees shed some or all their leaves, resulting in fluctuations in canopy density. This allows more sunlight to reach the forest floor and consequently the development of dense ground and shrub layers, features that distinguish these forests from evergreen tropical forests. Diurnal and monthly fluctuations in temperature are far greater than those in evergreen forests. Mean monthly minimum temperatures can drop to 15°C and mean monthly maxima may exceed 35°C. The greatest expanses of seasonal tropical forest grow in eastern Brazil (cerrado), India (monsoon forests), the Zaire Basin and East Africa.
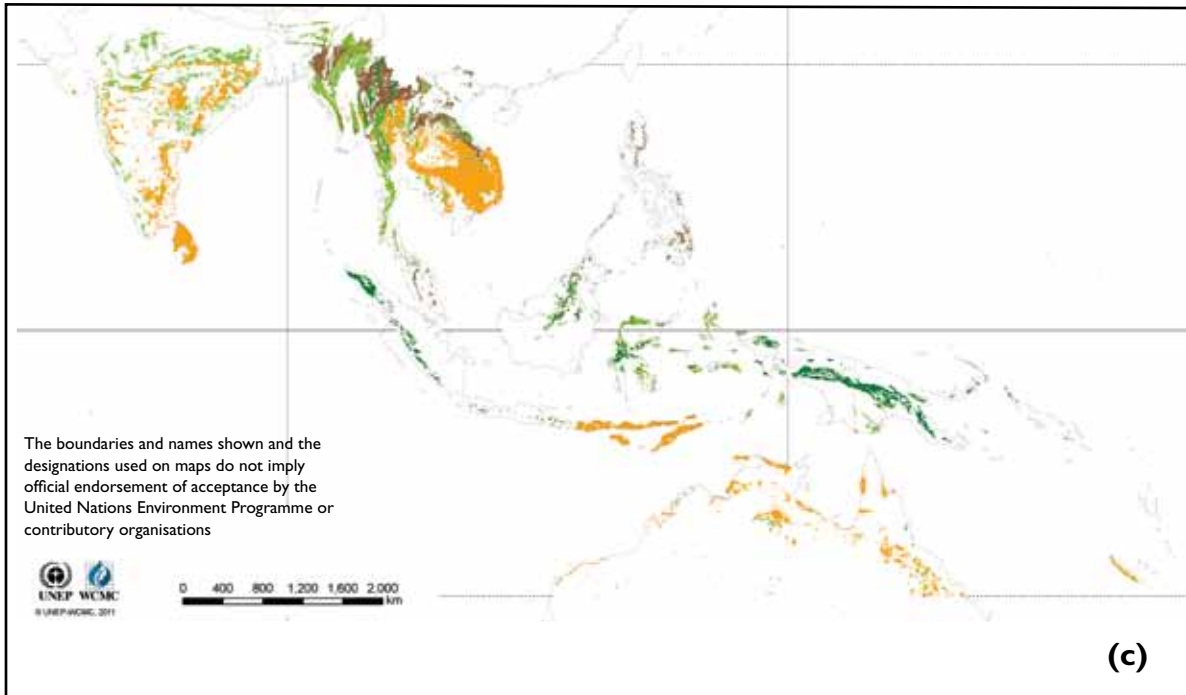
Seasonally dry tropical forest in northern Thailand. Around half the tree species are deciduous and half are evergreen. The stream runs dry in the hot season.

Both evergreen and deciduous tree species grow closely together, forming a continuous main canopy of up to 35 m tall. Structural features shared by seasonal and evergreen tropical forests include emergent trees, buttressed trees, woody climbers and epiphytes, although they are all less prevalent in seasonal than in evergreen forests. The presence of bamboos distinguishes seasonal forests from evergreen forests. Seasonal tropical forests retain a high degree of structural complexity, although the stratification of the canopy is usually not as highly developed as that in evergreen forests. They are usually less diverse than evergreen forests, although their tree species richness can match that of evergreen forests in some places (Elliott *et al.*, 1989). Although animals remain the main pollinators and seed dispersers in seasonal tropical forests, wind pollination and seed dispersal are more common than in evergreen tropical forests. Seasonal tropical forests may be more resilient to global warming than evergreen forests because their flora and fauna have evolved to cope with seasonal drought.

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(b)

Tropical dry forest
Upper montane forest
Lower montane forest
Seasonal forests (Semi-evergreen moist broadleaf forest)

Seasonal forests (Deciduous/semi-deciduous broadleaf forest)
Disturbed natural forest
Water bodies

Extent of tropical dry, seasonal and montane forests of a) Central/South America b) Africa and c) Asia, based on UNEP–WCMC's classification of 1990, derived from a number of different national and international sources. The scales and dates vary between sources, and this synthesis can be considered to show global cover in approximately 1995. © UNEP–WCMC, 2011.

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Challenges to restoring seasonal tropical forests

Very little is known about the phenology, propagation and silviculture of the vast majority of tree species in these forests: clearly a problem when planning tree planting. In seasonally dry climates, trees can only be planted at the beginning of the rainy season because sufficient time must be allowed for their roots to grow deep enough to enable them to survive the first dry season. So, nursery work schedules must be devised to grow trees to a plantable size by the start of the rainy season, regardless of when seeds are produced or how fast seedlings grow. This requires a lot of research on tree phenology, seed germination and seedling growth.

Bamboos present one of the greatest challenges to the restoration of seasonal tropical forests because they suppress the growth of trees that are planted nearby. Their dense root systems fully exploit the soil, they cast dense shade and, in the dry season, they smother nearby tree seedlings with a dense layer of leaf litter. Therefore, controlling (but not eliminating) bamboos is essential for successful restoration of seasonal tropical forests. Luckily, bamboo canes and bamboo shoots are useful products, so local people usually need no encouragement to harvest them.

In some degraded seasonal tropical forests, the rich soils will have been severely depleted and are consequently low in organic matter and minerals such as phosphorous. These soils may require the addition of organic matter and/or inorganic fertiliser for tree seedlings to establish and flourish.

Invasive plants and browsing by domestic livestock are both big problems in seasonal tropical forests that must be addressed by working with local people. Seasonal tropical forests are more fire-prone than evergreen forests, so weeding, firebreak construction and an effective fire prevention program are all particularly important when restoring these forest types.

Box 2.4. Bamboos.

As aggressive giant grasses, bamboos can suppress tree establishment, but they are also a natural component of seasonally dry tropical forests and a source of several forest products. Many species exhibit mass flowering at intervals of years or decades, after which the plants die back.

Bamboos are giant 'woody' grasses in the family Poaceae, with more than 1,400 species growing mostly in the tropics and sub-tropics. They are pan-tropical with the Asia–Pacific region having the most species (1,012, with 626 in China alone) and Africa the fewest. The largest bamboos grow up to 15 m tall and have stems that reach 30 cm in diameter. They are the world's fastest-growing woody plants and are among the most useful. Bamboo canes are used for all kinds of temporary construction and furniture and are split and woven to make mats and baskets, whereas young culm buds ('bamboo shoots') are a popular vegetable in oriental cuisine.

Bamboos are classified into two types: 'clumping' and 'running'. Running bamboos produce very long, rhizomes that can spread considerable distances underground. Each rhizome node can produce a new shoot, from which a new rhizome system can develop. This characteristic is sometimes beneficial, e.g. for controlling soil erosion, but it also enables these plants to become invasive and to suppress tree establishment and growth. If forest restoration is threatened by invasive bamboos, the bamboos must be controlled. Cutting back the shoots may be effective, but if it is not followed up rigorously, it actually stimulates the spread of the rhizomes underground. Therefore, a systemic herbicide such as glyphosate (Roundup) can be applied to the cut culm stumps to kill the rhizomes. Bamboos are characteristic features of some seasonal tropical forest types so, although it may be necessary to suppress them during initial tree establishment, they should be allowed to re-grow afterwards.

Dry tropical forests

Dry tropical forests are most common at 12–20° latitude from the equator, where annual rainfall is 300–1,500 mm and the dry season lasts 5–8 months. Such forests often grow closely inter-mingled with seasonal forest types. Abrupt transitions between the two are usually the result of fire history or variations in soil moisture. The most extensive dry tropical forests are the drier type of miombo and Sudanian woodlands in Africa, caatinga and chaco in South America, and deciduous dipterocarp forest in Asia. Structurally, dry tropical forests are simpler than wetter tropical forests. They are predominantly deciduous, with an irregular and sometimes discontinuous canopy, up to 25 m high, that allows the development of a rich and varied ground layer, which is sometimes dominated by grasses. Large emergent trees, buttresses and bamboos are absent. Woody climbers and epiphytes occur infrequently but vines are more common. Dry tropical forests share many of the families and genera of plant species found in wetter tropical regions, but most of the species are different. They are less species-rich than wetter tropical forests but are home to many species that live in no other forest type (habitat endemics); this is especially true of coastal dry forests.

Dry tropical forests have a prevalence of conspicuously flowered trees (which often flower when leafless) that are pollinated by specialist bees, hawk-moths and birds (hummingbirds in the Neotropics and, to a lesser extent, sunbirds and flower-peckers in the Old World tropics). Seeds are wind-dispersed for up to one third of trees and up to 80% of woody climbers (Gentry, 1995).

Challenges to restoring dry tropical forests

Dry tropical forests are perhaps the most endangered of tropical forest types (Janzen, 1988; Vieira & Scariot, 2006) with only 1–2% of their original area remaining intact (Aronson *et al*., 2005). They are a lot easier to clear than evergreen forests, so they have been subjected to longer and more intense degradation, including logging, chopping for fire wood, burning and cattle browsing.

Tree planting is possible only during a short window of opportunity at the beginning of the rainy season and the growing season for root development is short (usually less than 6 months before the onset of the dry season). It is important, therefore, that only high-performing tree species are planted, and these may be more difficult to find than in other tropical forests because there are fewer tree species from which to choose. Fruiting

Few epiphytes grow in dry forests and those that do are highly drought tolerant; examples include *Dischidia major* (top) and *D. nummularia* (bottom) (Apocynaceae), pictured here growing on *Shorea roxburghii* (Dipterocarpaceae) in northern Thailand. *Dischidia major* harvests nutrients that are released by the activities of the ants that it hosts its hollow leaves.

Acacia-dominated
dry woodland,
Kenya
(Photo: A. McRobb)

is more seasonal than in wetter forest types, seed dormancy is more common, and seedlings may grow more slowly in the nursery. All of these factors present challenges to nursery tree production in the dry tropics and require considerable research.

The greatest impediments to the restoration of dry tropical forests, however, are the hot, dry climate, poor soils and fire. The sites that are available for restoration are mostly those too infertile for agriculture (Aronson *et al.*, 2005). Soils are often lateritic and hard, so digging holes for tree planting is hard work and expensive. In the dry season, the upper soil layers dry out quickly. In the rainy season, they become waterlogged because of poor drainage, suffocating the roots and killing planted trees. Such problems may be overcome by soil amelioration before planting trees, e.g. use of green manure, adding water-absorbing polymer gels to planting holes, watering trees immediately after planting and applying organic mulch. All such measures may reduce post-planting mortality but they also add to the costs. Weeds grow relatively slowly at dry sites, so weeding may be needed less frequently than at wetter sites, but frequent and liberal application of fertiliser is essential throughout the first 2–3 growing seasons.

Dried grasses and leaf litter provide ideal fuel for fire. Therefore, fire prevention measures are particularly important when restoring dry tropical forests. Other intense human pressures include the introduction of invasive plant species and cattle browsing. Outreach programs for local people are essential in tackling these problems. Nonetheless, in some places, the resilience of disturbed dry forests can be high enough for forest recovery to be initiated simply by preventing fires and removing cattle (see **Section 5.1**).

Tropical forests on mountains

With increasing elevation in the tropics, rainfall usually increases while mean temperatures fall (on average by 0.6°C for every 100 m ascended), resulting in lower evapotranspiration rates and slower decomposition rates. Organic matter therefore accumulates in soils at higher elevations, increasing their water-holding capacity. Consequently, forests on mountains are cooler and wetter than those on adjacent lowlands, and their structure, stature, species composition and leafing phenology can all change abruptly over short distances. In drier parts of the tropics, deciduous forests at the foot of mountains give way to mixed deciduous forests higher up, with evergreen forests being confined to upper slopes and summits. Floristically, ascending a mountain in the tropics is analogous to travelling away from the equator: the tree genera typical of tropical lowlands are gradually replaced by those more usually associated with temperate forests.

Forests on mountains have traditionally been divided into 'lower' and 'upper' montane forests, although the transition between the two is often floristically indistinct and the elevation at which they occur is highly variable, depending on latitude, topography and prevailing climate. The most extensive montane tropical forest ecosystems grow in the Eastern tropics and on the Andes in South America. Montane forests are least extensive in Africa, where they can be found in Cameroon and along the eastern fringe of the Zaire Basin.

Lower montane forest, northern Thailand

Lower montane tropical forests

The transition from lowland to lower montane forest is gradual and can occur anywhere between 800 and 1,300 m elevation. Lower montane forest is largely evergreen in the wetter tropics or mixed evergreen and deciduous at more seasonal latitudes. The trees tend to be shorter than those of lowland forests (15–33 m tall) with few or no emergents. Buttresses, cauliflory and lianas are less evident, whereas epiphytes are more common. Species diversity is generally high because variations in elevation, aspect and slope can result in sharp changes in rainfall, wind direction and temperature.

Upper montane tropical forests and cloud forests

The most dramatic change in montane forests occurs where the mountains meet the clouds: above 1,000 m on coastal and insular mountains or above 2,000–3,500 m inland. Drenched in persistent or frequent mist, 'cloud forests' (also referred to as 'elfin' or 'mossy' woodlands) are characterised by stunted, crooked trees with gnarled trunks and branches (usually smothered in epiphytes) and compact

Cloud forest, Irian Jaya (Photo: A. McRobb)

crowns, composed of small, thick leaves. Although species diversity is generally lower here than in lower montane forests, levels of endemism are high because habitat-specific plant and animal populations evolve in genetic isolation.

Organic matter accumulates in the soils (because decomposition occurs slowly in the cold montane climate) making them highly acidic. Rainfall is high, but up to 60% of the water reaching the soil may come from mist droplets that are captured by the tree crowns (termed 'fog drip' or 'cloud stripping'). Furthermore, the organic-matter-rich soils of upper montane forests have very high water-storage potential, making such forests the most important catchment areas for the water supplies of many tropical countries. Despite this, cloud forests are now among the world's most threatened terrestrial ecosystems (Scatena *et al.*, 2010). Across Central America and the South American Andes, cloud forests are being cleared for subsistence farming and horticulture, despite their poor soils and rugged terrain. In the Americas and Africa, cloud forests continue to be cleared for rearing livestock. Other threats include logging, fuel-wood harvesting, fire, mining, road construction and hunting.

Table 2.1. General characteristics of forests on mountains in the humid tropics (adapted from Whitmore (1998)).

Characteristic	Lowland	Lower montane	Upper montane
Canopy height	25–45 m	15–33 m	1.5–18 m
Emergent trees	Characteristic (to 60 m tall)	Often absent (to 37 m tall)	Usually absent (to 26 m tall)
Pinnate leaves	Frequent	Rare	Very rare
Leaf size (woody plants)	Mesophyll	Mesophyll	Microphyll
Buttresses	Frequent, large	Rare, small	Usually absent
Cauliflory	Frequent	Rare	Absent
Large woody climbers	Abundant	Less abundant	Rare or absent
Vascular epiphytes	Frequent	Abundant	Frequent
Bryophyte epiphytes	Occasional	Common	Abundant

Challenges to restoring montane tropical forests

Working on steep, wet tropical mountains is beset with logistical problems. Access is often the greatest obstacle. Poor roads and the need for 4-wheel-drive vehicles can greatly increase restoration costs. Periodic landslides block roads and smother restoration sites, and soil erosion is a continuous problem. Nothing short of major engineering works can prevent landslides, but soil erosion may be reduced (on a small scale) by applying mulch.

Low temperatures slow the growth of planted trees, and in depressions and gullies, frost can kill them in the winter. The closer tree crowns are to the ground, the greater is the risk of frost damage. Fast-growing trees, which elevate their crowns above the danger zone, are therefore less prone to frost damage. Cutting back weeds from around planted trees reduces the height at which cold air collects. Pulling mulch away from the trunks of very young trees and wrapping them with newspaper may also help to reduce the risk of frost damage.

The exposure of planted trees to strong winds is also a particular problem on mountains. A long-term solution can be to plant the first trees as strategically placed wind breaks. The wind breaks then protect subsequently planted trees from exposure and can act as corridors for seed dispersers (especially if they are connected to remnant forest), thereby enhancing tree species recruitment (Harvey, 2000).

The extirpation of seed-dispersing animals from isolated or highly fragmented montane forests can seriously reduce the rate of seedling recruitment of new (non-planted) tree species into restored plots, and thus delay biodiversity recovery. Attracting seed-dispersing birds by planting rapidly maturing, fleshy-fruited trees (the framework species method (see **Section 5.3**)), or by placing artificial bird perches across restoration sites can help to alleviate the problem (Kappelle & Wilms, 1998; Scott *et al.*, 2000).

It has been predicted that large areas of agricultural land that formerly was cloud forest may be abandoned in Latin America as people move to urban areas, creating considerable opportunities for restoration (Aide *et al.*, 2011). Such areas can, however, develop into fire-climax grasslands, which prevent natural succession. Consequently, clearance of the grass vegetation may be necessary before the land can be planted with tree seedlings or directly seeded. Planting native cloud forest trees has been constrained by a lack of basic knowledge on the reproductive biology, seed handling, propagation and silviculture of most species (Alvarez-Aquino *et al.*, 2004).

Effects of substrate

The soil type and underlying rock can greatly affect the structure and species composition of tropical forest. For example, highly acidic (pH <4) and nutrient-poor podzols in South America and Southeast Asia support heath forest. Here, small, closely spaced, evergreen trees, often of a few dominant species, form a low, non-layered canopy of mostly microphyll species over dense woody undergrowth. Restoring such forests can be impeded by the highly acidic and erosion-prone sandy soils, which cause high mortality among planted trees and corrode metal tags attached to them for monitoring.

Heath forest,
Irian Jaya
(Photo: A. McRobb)

Limestone also supports unique and often species-rich vegetation, with many endemic species, mostly in the seasonal tropics of Southeast Asia and the Caribbean. The porous nature of limestone leads to year-round water shortages, resulting in stunted, xeromorphic, semi-deciduous forest and scrub, with low tree density. Precipitous terrain, shallow soils and high levels of endemism all present challenges to restoration. Water-logging of the substrate or inundation by fresh water, either seasonally or permanently, also generates unique forest types.

Confined to Southeast Asia, peat swamp forests (or 'moor forests') grow in low-lying flat areas, where the decomposition of dead organic matter is slowed by water-logging. This results in the accumulation of acidic peat, eventually forming 'domes' of up to 20 km across and 13 m deep (Whitmore, 1998). Up to six forest communities are distinguishable growing in more or less concentric bands from the centre of the dome to its edge (Anderson, 1961). Each community has only a few tree species, but several are habitat-specific and sensitive to the water levels within the peat. This, along with the semi-fluid nature of the substratum, complicates restoration. When dry, peat is highly flammable and peat fires are notoriously difficult to extinguish. Therefore, hydrological recovery (i.e. 're-wetting' the peat by damming drainage channels) is often the first step to restoring peat swamp forests (Page *et al*., 2009). It prevents fires, preserves carbon stocks and creates better conditions for tree establishment.

Forest clinging to
limestone crags,
southern Thailand.
Water shortage is
the challenge to
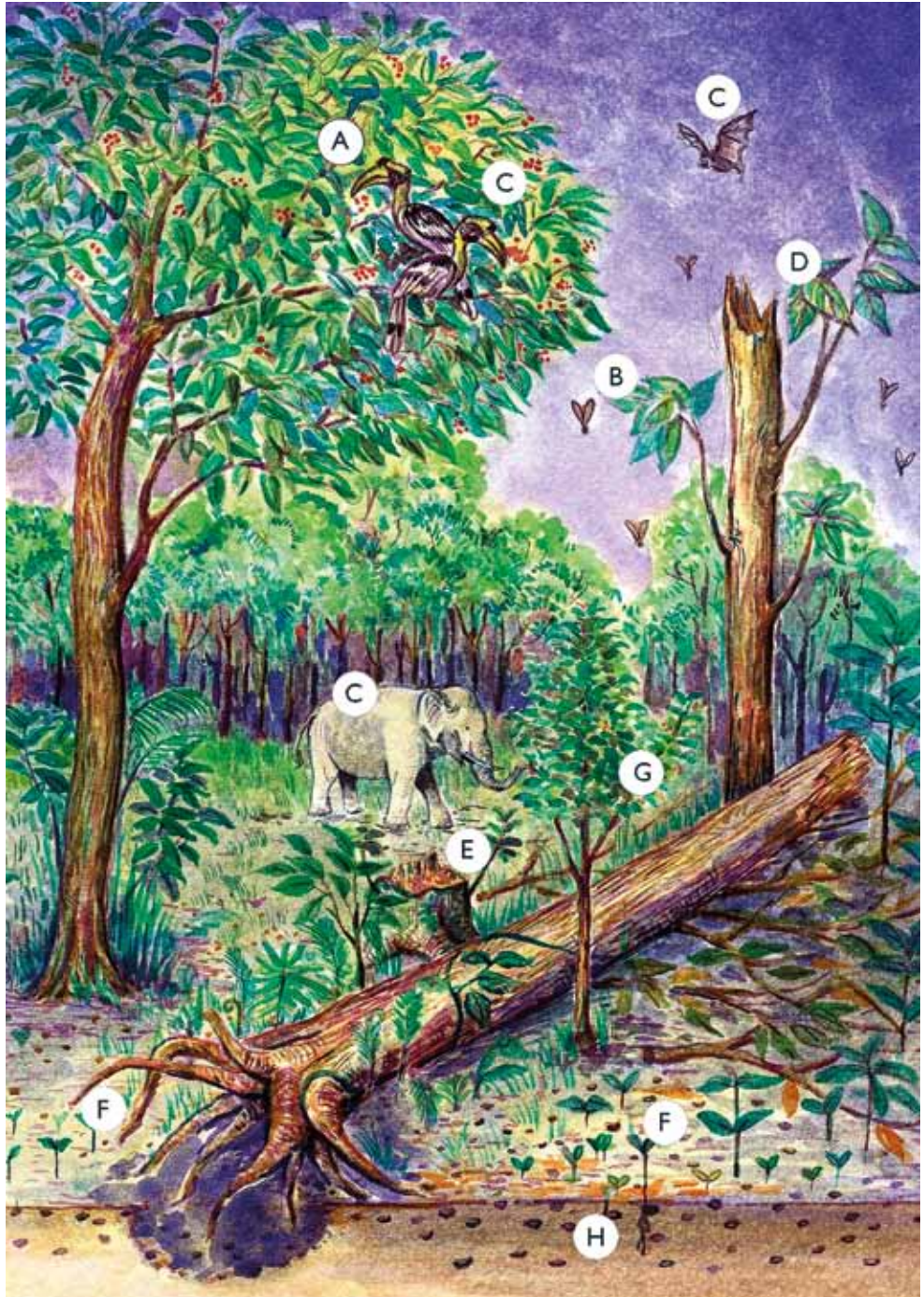plants growing in
this habitat.

Sago swamp forest, Irian Jaya (Photo: A. McRobb)

Fresh water swamp forests (or marsh forests) are a diverse range of forest types that are flooded periodically, in places up to 9 months of each year, growing most extensively alongside the world's largest tropical rivers (the Amazon, Congo and Mekong). In these forests, palms and dicotyledonous trees grow up to 30 m tall, often forming two canopy layers. The longer such forests are inundated each year, the lower is their tree species richness. Swamp forests rely on the accumulation of dead herbaceous vegetation before they can take root. Shrubs establish first, often followed by palms and later by larger trees. This results in a gradient of different forest types on moving away from open water. Taking such zonation into account by manipulating natural succession and/or by planting trees on flooded sites is highly problematic, but thanks to the high-nutrient soils, restoration can progress rapidly once tree establishment has been achieved.

In tropical estuaries and along coast lines, freshwater swamp forests give way to mangroves in the inter-tidal zone. Mangroves are dominated by a few species of salt-tolerant trees, often with characteristic pneumatophores (exposed roots for gaseous exchange) that allow the plants to overcome the anaerobic conditions in the sediment in which they grow. Like other swamp forests, mangroves are zoned into different forest types along a wet-to-dry gradient. Most produce water-dispersed seeds annually in large numbers and some are viviparous (i.e. the seeds germinate on the tree before dispersal). Restoration projects on tidal mudflats are both difficult and dangerous. Planting propagules or small seedlings has a very low success rate. Planting larger saplings is more expensive but more successful. Desiccation, high salinity and attacks by herbivorous insects being the most common problems (Elster, 2000).

Mangrove forest, Irian Jaya (Photo: A. McRobb)

Succession proceeds rapidly in tree-fall gaps within intact forest. (A) Nearby fruiting trees provide (B) a dense seed rain. The surrounding forest provides habitat for (C) seed-dispersing animals. (D) Damaged trees and (E) tree stumps re-grow. (F) Seedlings and (G) saplings, which were formerly suppressed by the dense forest canopy, now grow rapidly. (H) Seeds in the soil seed bank germinate. In large deforested areas, many of these natural mechanisms of forest regeneration are reduced or blocked entirely by human activities.

Regional variations

The earlier account merely outlines the broadest tropical forest types. Within each of these, the forest classification schemes of individual countries distinguish many sub-types, often with inconsistent terminologies.

2.2 Understanding forest regeneration

Forest restoration is all about accelerating natural forest succession, so its success depends on understanding and enhancing the natural mechanisms of forest succession.
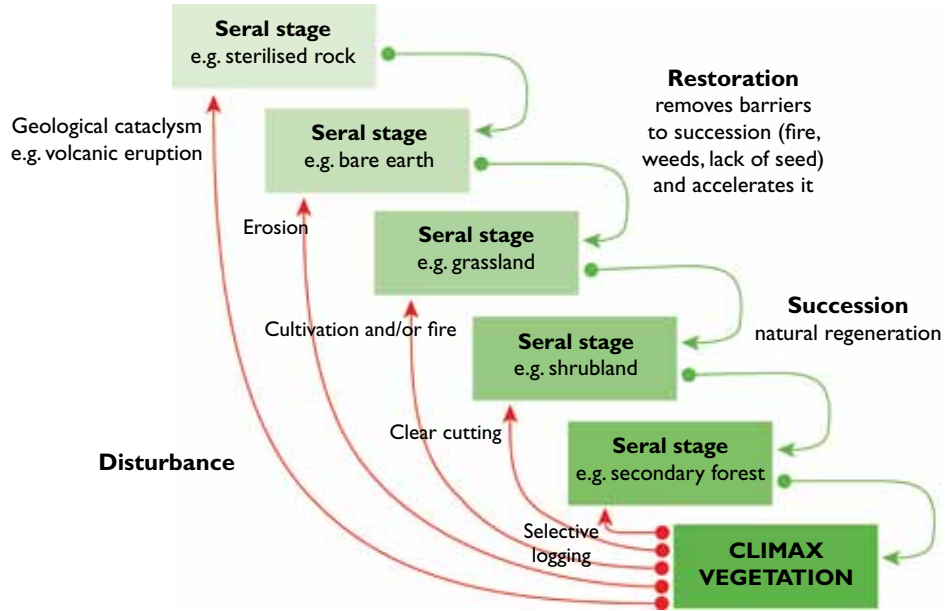
What is succession?

Succession is a series of predictable changes in ecosystem structure and composition that occurs after disturbance. If allowed to run its course, succession eventually results in a final, climax ecosystem with maximum biomass, structural complexity and biodiversity within the limitations imposed by the local soil and climatic conditions.

A climax tropical forest is not a stable unchanging system but rather a dynamic equilibrium undergoing constant disturbances and renewal. Gaps are formed when large trees die, but they are rapidly filled as saplings and seedlings grow up to exploit the light. Thus a climax forest is an ever-changing mosaic of differently sized tree-fall gaps, regenerating patches and old growth, with species composition varying according to micro-habitat, disturbance history, seed dispersal limitations and chance events. All of these factors contribute to the high species diversity that is characteristic of most climax tropical forests.

More widespread disturbance of climax forest causes it to revert to an earlier, temporary ecosystem or 'seral stage' in the successional sequence. The nature of the seral stage depends on the severity of the disturbance. A major disturbance, such as a volcanic eruption, completely destroys the plant community and soil, causing the land to revert to the earliest seral stage: bare rock. Less severe disturbances, such as logging, cultivation and fire, turn forests into grass- or shrub-lands. Once disturbance ceases, sequential changes in species composition occur due to interactions among plants, animals and their surrounding environment. Bare rock becomes colonised by lichens and mosses, a process known as 'primary succession'. Grass- and shrub-lands undergo 'secondary succession', whereby shrubs shade out herbs, light-demanding pioneer trees shade out shrubs, and much later, pioneer trees are themselves shaded out by shade-tolerant climax trees. Thus, the forest becomes progressively denser, more structurally complex and more species-rich as succession propels it towards the climax condition.

Even under the best of conditions, this process may take 80–150 years to complete, and more often than not, continued human disturbance completely prevents the attainment of climax forest. Therefore, active restoration is necessary wherever more speedy return to climax forest than would happen naturally is desirable.

Seral stage e.g. sterilised rock

Seral stage e.g. bare earth

Seral stage e.g. grassland

Seral stage e.g. shrubland

Seral stage e.g. secondary forest

CLIMAX VEGETATION

Geological cataclysm e.g. volcanic eruption

Erosion

Cultivation and/or fire

Clear cutting

Selective logging

Disturbance

Restoration removes barriers to succession (fire, weeds, lack of seed) and accelerates it
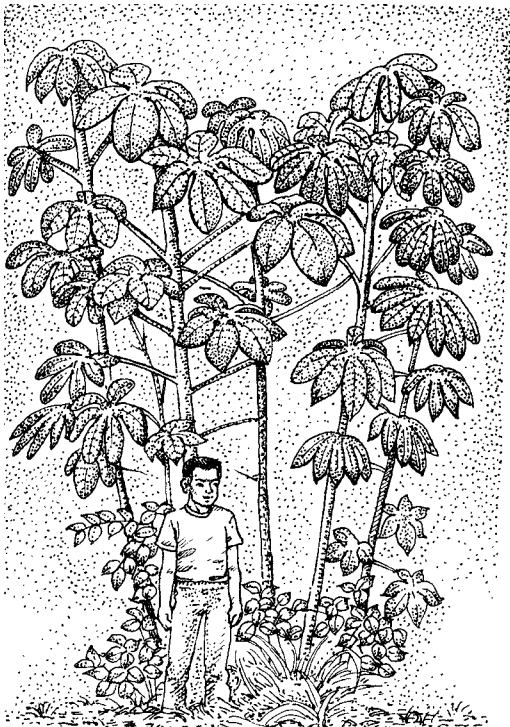
Succession natural regeneration

Understanding forest succession is essential for designing effective forest restoration methods. Forest restoration seeks to remove those factors that prevent natural forest succession from progressing.

Pioneer and climax tree species

Tree species can be divided into two broad groups, depending on when they appear in the sequence of forest succession. Pioneer tree species are the first to colonise deforested sites, whereas climax forest tree species establish later, only after the pioneers have created shadier, cooler and wetter conditions. The main distinctions between the two groups are that seeds of pioneers can germinate only in full sunlight and their seedlings cannot grow in shade, whereas the seeds of climax trees can germinate in shade and their seedlings are shade-tolerant.

Cecropia, the largest genus of pioneer trees in the neotropics

The seeds of pioneer trees can lie dormant in the soil, germinating when a gap is formed and light intensity increases. Once the forest canopy closes, however, no more seedlings of pioneer species can grow to maturity. Therefore, pioneer trees grow rapidly and usually produce large numbers of small fruits and seeds at a young age. These are dispersed over long distances by wind or small birds, thereby finding new disturbed areas to colonise. Pioneer species can be divided into two groups: early pioneers (e.g. *Cecropia*, *Macaranga*, *Trema*, *Ochroma*, *Musanga*, *Acronychia* and *Melochia*) and late or persistent pioneers (e.g. *Acacia*, *Alstonia*, *Octomeles*, *Neolamarckia*, *Terminalia* and *Ceiba*). The former are the first species to colonise open areas but seldom live longer than 20 years, whereas the latter grow for 60–80 years and may persist even after climax tree species have begun to reach the canopy (although their seedlings are absent from the ground layer).
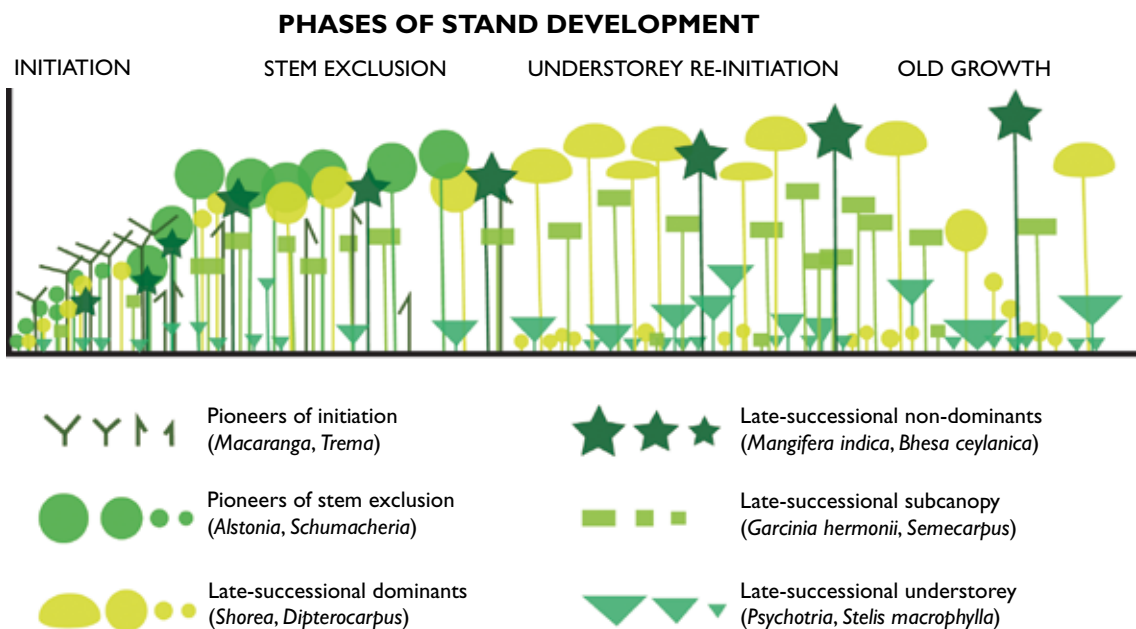
Climax tree species grow slowly over many years, gradually consolidating their position in the forest before flowering and fruiting. They tend to produce large, animal-dispersed seeds with low (or no) capacity for dormancy and large food reserves that can sustain seedlings in shaded conditions. Hence, climax tree species can regenerate beneath their own shade, giving rise to the relatively stable species composition of climax forest. They may live for hundreds of years.

In reality, the division between pioneer and climax tree species may be too simplistic. Many climax tree species grow very well when planted in deforested sites. Their absence from such areas is often not because they are limited by the hot, dry, sunny conditions of deforested sites but because their large seeds fail to be naturally dispersed into such areas. Most climax forest tree species are shade-*tolerant* but not shade-*dependent*. This means that tree-planting programs need not be restricted to pioneer species. Planting carefully selected climax tree species alongside pioneers 'short-circuits' succession and achieves a climax forest more rapidly than would happen naturally.

Ashton *et al*. (2001) provide a more refined view of the successional status of tree species by recognising six tree guilds. Short-lived 'pioneers of initiation' (i.e. early pioneers) are the first trees to form a canopy that shades out weeds. 'Pioneers of stem exclusion' (i.e. late or persistent pioneers) rise to dominate the canopy later. They live on while late successional (i.e. climax) canopy tree species grow up alongside them, forest biomass increases, and the tree species composition and structure of the forest become more diverse. The seedlings of pioneers disappear with the development of an understorey, marking a crucial milestone in the progress of succession. Ashton *et al*. (2001) subdivide late successional tree species into four groups, depending on the position of their crowns in the canopy: dominant (abundant in the main canopy or as emergent trees), non-dominant (less abundant in the main canopy), sub-canopy and understory. All six guilds may be present as seedlings early in succession (if seed dispersal is not limiting). If practicable, forest restoration should, therefore, attempt to mimic this by including representative species from all six tree guilds amongst those tree species planted or encouraged to regenerate.

Phases of stand development (adapted from Ashton *et al*. (2001))

PHASES OF STAND DEVELOPMENT

INITIATION · STEM EXCLUSION · UNDERSTOREY RE-INITIATION · OLD GROWTH

Pioneers of initiation
(*Macaranga*, *Trema*)

Pioneers of stem exclusion
(*Alstonia*, *Schumacheria*)

Late-successional dominants
(*Shorea*, *Dipterocarpus*)

Late-successional non-dominants
(*Mangifera indica*, *Bhesa ceylanica*)

Late-successional subcanopy
(*Garcinia hermonii*, *Semecarpus*)

Late-successional understorey
(*Psychotria*, *Stelis macrophylla*)

Limitations to natural reforestation

Disturbance beyond a certain 'threshold' can disrupt the usually efficient ecological mechanisms of forest recovery, causing the vegetation to enter into an 'alternate state'. A good analogy is provided by the elastic band. After moderate stretching, the band can easily return to its original ring shape. However, stretch the band too much and it breaks, becoming a short strip of stretchy rubber, i.e. an alternate state. The properties that enabled it to revert to a ring have been destroyed. It will never recover its original ring shape without human intervention to tie the two ends back together and restore the ring.

By analogy, deforestation on a large scale, followed by continuous disturbance, destroys the natural mechanisms of succession that enable forest recovery. Large deforested areas often become occupied by a persistent pre-climax seral stage (termed 'plagioclimax'), such as grassland, or by a completely new community dominated by invasive exotic species. Where human actions block succession, human intervention is needed to reinstate the mechanisms of forest recovery and allow succession to proceed towards the climax state.

Models of 'threshold dynamics' seek to explain and predict such irreversible changes. They show how 'positive feedback' mechanisms restrain the ecosystem in its degraded state, even after the disturbance has ceased. For example, cutting the trees in a tropical forest increases light levels, leading to an increase in grass cover. Hot, dry grasslands burn more easily than cool moist forest, giving rise to more fires that destroy establishing tree seedlings. This new fire regime prevents the site from reverting to forest, even if tree cutting is stopped.

Understanding such thresholds and the feedback mechanisms that cause forest ecosystems to remain in a persistent degraded state is very helpful in devising appropriate forest restoration strategies.

Regeneration in large deforested areas

In large deforested areas, the establishment of forest trees usually depends on the availability of local seed sources and the dispersal of seeds into deforested sites. Seeds must land where conditions are suitable for germination and they must escape the attention of seed-eating animals, the so called 'seed predators'. After germination, tree seedlings must win an intense competition with weeds for light, moisture and nutrients. Growing trees must also avoid being burnt by wildfires or eaten by cattle.
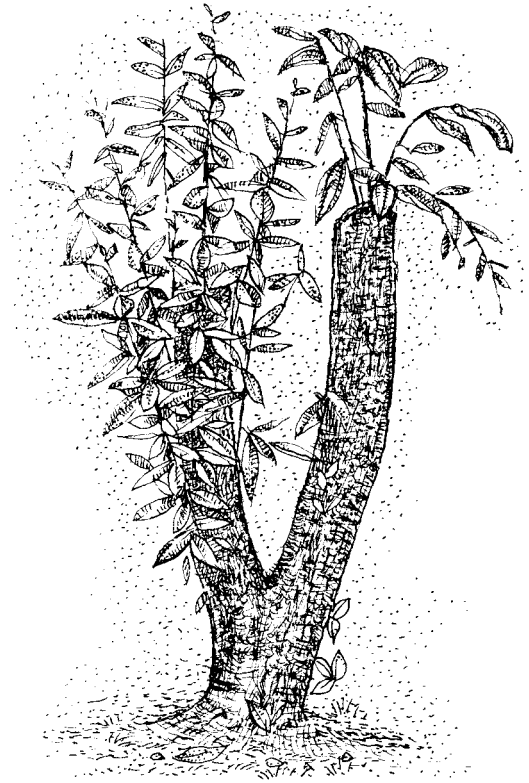
Limitations to regeneration from the seed bank

When a forest is cut down, large numbers of seeds remain in the soil (the seed bank). However, the vast majority of tropical tree species produce seeds that are viable only for short periods. So, if a forest is cleared and the site is then burnt and cultivated for more than a year or so, most seeds from the original climax forest seed bank die, because they have either no capacity for dormancy (Baskin & Baskin, 2005) or capacity for only a very short period of dormancy (i.e. they must germinate within 12 weeks (Forest Restoration Research Unit, 2010; Garwood, 1983; Ng, 1980)). Consequently, forest regeneration depends almost entirely on seeds that are dispersed into deforested sites from surviving forest remnants or from isolated trees in the surrounding landscape.

Coppicing

Some tree species can re-grow from old tree stumps or root fragments years after the original tree was chopped down (Hardwick *et al*., 2000). Dormant buds around the root collar of a tree stump can sprout spontaneously, often generating several new shoots. This is called coppicing. Examples of both climax and pioneer tree species can re-grow in this way. Drawing on food reserves that are stored in the roots, coppicing sprouts can rapidly grow above surrounding weeds and have greater resilience to fire and browsing than seedlings. Larger stumps tend to produce more vigorous shoots in greater numbers than smaller stumps. Furthermore, taller stumps survive fire, browsing and weed competition better than shorter ones because the shoots are usually above the height of the disturbance. Protecting tree stumps, therefore, gives forest regeneration a head start.

However, tree species that regenerate from stumps usually represent only a small proportion of the climax forest tree community. Although such trees can accelerate the recovery of forest structure, incoming seed is still essential to restore the full tree species richness of the climax forest.

Tree stumps are a major source of natural regeneration, particularly in recently logged over forests.

The importance of seed trees

All trees start life as seeds, so forest succession ultimately depends on the presence of fruiting trees nearby. In a largely deforested landscape, some tree species might be represented by a few scattered, isolated, individuals that somehow escaped the chainsaw, or there may be remnant forest patches producing seeds of a wide range of tree species. Fruiting trees not only provide seeds for forest regeneration, they also attract frugivorous seed-dispersing animals. In a deforested landscape, therefore, the protection of any remaining mature trees greatly enhances natural forest regeneration.

Seed rain

The seed rain consists of all seeds falling on to any particular site, either blown there by the wind or deposited by animals. The density and species composition of the tree seed rain on any deforested site depends on the nearness of fruiting trees and on the efficiency of seed-dispersal mechanisms. The seed rain is most dense and contains most tree species near to intact forest and is sparse in the centre of large deforested areas. A depleted seed rain is one of the most important causes of lack of forest regeneration or low species richness among the tree communities colonising deforested sites. Encouraging seed dispersal is, therefore, a vital element of forest restoration.

Wind-dispersal of tree seeds

In the wet tropics, relatively few tree species produce wind-dispersed seeds. Those that do are usually the tallest trees in the forest, often emergents (e.g. dipterocarps). Wind-dispersal is more common in the seasonal or dry tropics, but even there, less than half of tree species are wind-dispersed (although these species may account for up to 60% of individual trees (FORRU, 2006)).

Wind-dispersed seeds tend to be small and light, and they often have wings or other structures that slow their fall, enabling them to drift on air currents. Most are deposited within a few hundred metres of the parent tree, but some are uplifted by gales and transported over many kilometres. To maximise their dispersal distances, many wind-dispersed tropical tree species fruit at the end of the dry season, when mean maximum wind-gust speeds are at their highest. Consequently, wind-dispersed tree species are capable of colonising deforested sites up to 5–10 km from seed sources. If site conditions allow such species to become naturally established, there may be little need to include them in tree planting programs.

Seed dispersal by animals

With species living in all tropical regions, fruit-eating pigeons are the 'work horses' of natural forest regeneration, due to their seed dispersal capability. Here, wedge-tailed green pigeons feast on the fruits of *Hovenia dulcis*.

Most tropical tree species depend on animals for seed dispersal. Animals that eat fruits either discard the seeds or swallow them, later regurgitating or defecating them some distance from the parent tree (termed 'endozoochorous' dispersal). Fruits that contain animal-dispersed seeds tend to be brightly coloured to attract animals and fleshy, providing a food reward to their animal dispersers.

The dispersal of seeds from forest trees into deforested sites depends on animals that regularly move between the two habitats. Unfortunately, rather few forest animals venture out into open areas for fear of exposing themselves to predators. Apart from birds and bats, few animals travel far between eating a fruit and depositing the seed. Furthermore, many seeds are crushed by teeth or destroyed by digestive juices.

The maximum size of seeds that can be dispersed by an animal depends on the size of the animal's mouth. Small animal species are still relatively common in the tropics, but most of the larger ones, capable of dispersing large seeds, are now rare or have been hunted out. In the past, large herbivores were undoubtedly the most important dispersers of seeds from forest into deforested areas. Elephants, rhinos, tapirs, wild cattle and some deer often consume fruit in the forest, before emerging into open areas at night to graze or browse. With their large mouths, long retention times and long roaming distances, such animals can swallow the largest of seeds and transport them over long distances. The elimination of most of these large mammals over much of their former ranges in recent decades is now preventing the dispersal of many tree species with large seeds (Stoner & Lambert, 2007).

Because birds and bats can fly, they can disperse seeds over long distances. Forest birds such as macaws, parrots, hornbills, pigeons, fruit doves, fruit crows, jays, tityras

and bulbuls are particularly important because some species in these groups are equally at home in both forest and deforested sites and can disperse seeds between the two. Fruit bats are also important seed dispersers because they fly over long distances and drop seeds in flight. Unlike most birds, however, bats are nocturnal and cannot be identified using binoculars. Consequently, little research has been done on their role in forest regeneration. Research on bats is, therefore, a high priority for the improvement of forest restoration techniques. Non-flying mammal species that remain relatively common and are likely to disperse seeds between forest and degraded areas include wild pigs, monkeys, deer, civets and badgers, but again, largely because of their nocturnal habits, very little information is available on the seed-dispersing capabilities of these animals.

How far are seeds dispersed?

Most tree seeds fall within a few metres of the parent tree, and the density of a single tree's 'seed shadow' declines steeply with distance away from the tree. Neverthless, according to Clark (1998), approximately 10% of tree seeds are dispersed over much longer distances of 1 to 10 km. Little is known about long-distance seed dispersal because it is very difficult to measure, but it is vital for biodiversity recovery in any restoration site that is more than a few hundred metres away from intact forest. In the absence of natural long-distance seed dispersal, humans may have to collect seeds from forest and 'disperse' them into sites targeted for restoration in order to restore the climax forest tree community. Human-assisted seed dispersal may be the only way to ensure that large-seeded tree species are represented in restored forests.

Seed predation

A single tree produces vast numbers of seeds during its lifetime, although to replace itself, it need produce only one seed that eventually grows into a reproductively mature adult. The need for such excessive seed crops is because most seeds either fall where conditions are unfavourable for germination or are destroyed by animals. The rich food reserves contained within seeds make them nutritious meals for animals. Some seeds might pass through the digestive tracts of animals intact, but many others are crushed by teeth and digested.

Seed predation is the destruction of a seed's potential to germinate when an animal crushes or digests its embryo. It can occur when seeds are still attached to the parent tree (pre-dispersal predation), but it has most impact on forest regeneration when seeds that have already been dispersed into deforested areas are eaten (post-dispersal predation).

Levels of seed predation

Seed predation can seriously limit natural forest regeneration. Levels of seed predation are highly unpredictable, varying from 0% to 100%, depending on tree species, vegetation, location, season and so on. In deforested sites, seed predation is usually severe enough to reduce significantly the seed survival of most tree species (Hau, 1999), but levels decline as canopy closure is achieved and forest regeneration progresses. Seed predation significantly affects both the distribution and abundance of tree species. It is also a potent evolutionary force, compelling trees to evolve various morphological and chemical mechanisms to defend their seeds against attack, e.g. poisons, tough seed coats and so on.

Animals that eat seeds in regenerating forests

Small rodents and insects, particularly ants, are the most abundant seed predators, capable of affecting forest regeneration (Nepstad *et al.*, 1996; Sanchez-Cordero & Martínez-Gallardo, 1998). Rodents thrive in the weedy, herbaceous vegetation that dominates most deforested sites, but populations decline as soon as canopy closure begins to shade out the weeds (Pena-Claros & De Boo, 2002). Younger successional stages also support higher densities of ants than more advanced regeneration (Vasconcelos & Cherret, 1995).

Susceptibility of seeds to predation

Ecological theory suggests that the susceptibility of any particular tree species to seed predation depends on the food value of its seed. Animals should consume seeds that provide them with maximum nutriment while requiring the least effort to find them. Most attention has been paid to the influence of seed size on vulnerability to predation. Large seeds provide large food rewards to those seed predators that are capable of processing them. Animals may be able to locate large seeds easily, because they are more visible and emit more odour than small seeds, but small rodents have difficulty handling very large seeds. By contrast, small seeds have low food value and are easily overlooked (Vongkamjan, 2003; Mendoza & Dirzo, 2007; Forget *et al.*, 1998). The longer a seed lies on the ground before germinating, the greater is the probability that a predator will discover it. Consequently, seeds that have longer periods of dormancy usually suffer greater predation rates.

The nature of the seed coat is important in protecting seeds from predation. A tough, thick and smooth seed coat makes it very difficult for rodents to reach the nutritious seed contents. Low predation rates amongst seeds that have thick or hard seed coats have been reported for many forest tree species (e.g. Hau, 1999; Vongkamjan, 2003). There may be a trade-off, however, between the effects of seed coat thickness and length of dormancy on seed predation. A thick seed coat often causes prolonged dormancy, which lengthens the period during which seeds are available for attack by predators. But even the toughest seed coat must soften just before germination, presenting a window of opportunity for seed predators. Vongkamjan (2003) observed that several hard-coated tree seed species are attacked during this vulnerable period.

The teeth of rats make short work of large seeds, but rats can act as dispersers of tiny seeds.

Dispersal pattern may also affect the likelihood of predation. Seeds that are scattered thinly over a large area (a pattern that often results from wind-dispersal) are hard for predators to find, whereas a clumped dispersal pattern (characteristic of animal-dispersal) means that once one seed has been discovered, the whole clump will probably be predated. Sporadic large fruit crops can surmount this problem by satiating seed predator populations: seed predators cannot possibly eat all the seeds in such large crops, so many seeds escape predation.

When it comes to seed predation, the literature is full of contradictory statements and opposing viewpoints. The effects of seed predation undoubtedly depend on complex interactions among many variables, including the nature of the environment, the availability of alternative food sources and the individual preferences and seed handling capabilities of the particular seed predator species present. But seed predation is certainly a factor that must be considered in forest restoration projects, particularly those that include direct seeding. Models that can accurately predict the overall effects of seed predation have yet to be made; therefore, the effects of seed predation must be evaluated for each individual site.

Seed dormancy

After being deposited in a deforested site, a seed might not germinate immediately. The dormant period is the length of time during which a mature seed fails to germinate under favourable conditions. It enables seeds to be dispersed at the optimal time, survive the rigours of dispersal (such as being swallowed by an animal) and then germinate when conditions are favourable for seedling establishment.

In general, tree species that grow in cooler, drier climates are more likely to produce dormant seeds than those growing in warmer, wetter climates. Therefore, dormancy is more frequent among deciduous forest and montane tree species than among lowland evergreen forest tree species. In a survey of more than 2,000 climax tropical tree species in evergreen, semi-evergreen, deciduous, savanna and montane forests, Baskin and Baskin (2005) reported that 43%, 48%, 65%, 62% and 66% of species, respectively, exhibited dormancy periods of more than 4 weeks. Physiological dormancy (inhibited embryo development) is the most frequent mechanism of dormancy amongst evergreen, semi-evergreen and montane forest tree species, whereas physical dormancy (caused by impermeable seed coverings that restrict moisture absorption and gaseous exchange) is more prevalent among deciduous and savanna forest tree species.

Germination

The transition from seed to seedling is a dangerous time in a tree's life. Seed dormancy must end and appropriate levels of moisture and light must exist to trigger germination. Because of its small size, low energy reserves and low photosynthetic capability, a young seedling is very vulnerable to changes in environmental conditions, competition from other plants and attack by herbivores. A single caterpillar can completely destroy a young seedling in minutes, whereas larger plants are more resistant to attack.

Timing of seed germination

In the ever-wet tropics near the equator, where soil moisture is continuously high, conditions for seed germination remain favourable all year round. But in the seasonal tropics, the optimal time for tree seed germination is shortly after the start of the rainy season. Seedlings establishing during this period have the full length of the rainy season to build up energy reserves and grow their roots deep into the soil. An extensive root system enables seedlings to survive the desiccating heat of their first dry season by accessing moisture stored deep in the soil. Another reason for germination at the start of the rainy season is the release of soil nutrients at that time. Dry-season fires release nutrients as ash, which the first rains then wash into the soil. As soil moisture rises, the decomposition of organic matter accelerates, releasing yet more nutrients into the soil.

Although the number of germinating tree species peaks at the start of the rainy season, seed dispersal, at the tree community level, occurs throughout the year. This is because the optimal seed dispersal time for any individual tree species depends on a multitude of varying factors, such as the seasonal availability of pollinators, the time required to develop a mature fruit from a fertilised flower and the seasonal availability of dispersal agents. Variation among species in the length of seed dormancy allows each species to disperse its seeds at the optimal time and yet still germinate at the most favourable period, early in the rainy season. For example, seeds that are dispersed at the start of the rainy season tend to have very short dormancy or germinate immediately, whereas those dispersed six months earlier tend to have dormancy of around 6 months. This phenomenon has been well-documented for both Central America and Southeast Asia (Garwood, 1983; Forest Restoration Research Unit, 2006) and it is of crucial importance for the production of trees from seed in nurseries (see **Chapter 6**).

Conditions necessary for germination

Seed germination depends on many factors, the most important of which are sufficient soil moisture and adequate light conditions (not only total light levels, but also the quality of the light). Large, deforested sites, typically dominated by dense weeds, present a hostile environment to tree seeds. On these sites, temperatures fluctuate dramatically between night and day. Humidity is lower, wind speeds are higher and soil conditions are much harsher than those in a forest. Many seeds become trapped in the weed canopy, where they dry out and die, before even reaching the soil.

Even for seeds that penetrate through the weed canopy, weeds present another problem. A high ratio of red to far-red light stimulates the germination of many pioneer tree species, particularly those with small seeds (Pearson *et al*., 2003). By absorbing proportionately more red light than far-red light, a dense green canopy of weed foliage removes this vital stimulus. Therefore, the germination of most forest tree species depends on the presence of so-called 'germination micro-sites', where conditions are favourable. These are tiny sites with reduced weed cover and sufficient soil moisture to induce seed germination. They include decaying termite mounds, rocks covered in moss and especially rotting logs. The latter provide an excellent moist and nutrient-rich medium for seed germination and are usually weed free.

Rotting dead tree trunks provide excellent micro-sites in which tree seeds can germinate.

Animals can enhance seed germination

The passage of seed through an animal's digestive system can affect both total germination percentage and the pace of germination. For most tropical trees, passage through an animal's gut has no effect on germination, but for those species that show a response, germination is enhanced more often than it is inhibited. Travaset (1998) reported that ingestion by animals increased germination percentage of 36% of the tree species examined; it reduced germination percentage for only 7%. The seeds of 35% of the tree species included in the study germinated more rapidly after passage through an animal's gut; only 13% had delayed germination. Nevertheless, the responses are highly variable: the seeds of species within the same genus, or even from different individual plants of the same species, can have different responses. So, the consumption of seeds by animals can be essential for dispersal, but it is less important for enhancing germination.

Seedling establishment

After a seed has germinated, the greatest threats to seedling survival in deforested areas are competition with weeds, desiccation and fire.

Weeds can suppress regeneration

Deforested areas are usually dominated by a few species of light-demanding grasses, herbs and shrubs. These plants rapidly exploit the soil and develop a dense canopy, which absorbs most of the light available for photosynthesis. The abilities of a dense weed canopy to trap incoming seeds and to inhibit germination by altering light quality have already been mentioned. But even if seeds penetrate the weed canopy and germinate, the emerging seedlings are then overshadowed by the weeds and starved of light, moisture and nutrients.

Because trees evolved to grow tall, they must expend considerable energy and carbon to produce the woody substance, lignin, that supports their future massive size against gravity. Free of the need to make lignin, herbs can grow much faster than trees. Only when a tree's crown overshadows the surrounding weeds, and its root system

penetrates below that of the weeds, does a tree gain an advantage. At this point, light-demanding weeds are quickly killed by the shade cast by the tree, but weed competition usually kills most tree seedlings long before they over-top the weeds.

Weeds also prevent forest regeneration by providing fuel for fires in the dry season. Most herbaceous weeds survive fire as seeds, corms or tubers buried in the soil, or they (e.g. grasses) possess well-protected growing points that re-sprout after fire. In trees, the growing points are unprotected, raised on the tips of branches. In a fire, therefore, small seedlings are often completely incinerated by the blazing dried weeds surrounding them. Re-sprouting of older saplings is possible, but only after they are about 1 year old.

The weeds that are most capable of suppressing forest regeneration are nearly always exotic species that have been deliberately introduced and now flourish outside the ranges of their natural enemies. Many weeds in Africa and Asia originate from Central or South America. Several are in the families Leguminosae and Asteraceae (Compositae) and they usually share the following characteristics: i) they are rapidly growing perennials that flower and fruit at a very young age; ii) they produce very large numbers of seeds (or spores) that can survive in a dormant state and thus build up in the soil seed bank; iii) they are resilient after burning (even though their above-ground parts may be totally destroyed, they can regenerate rapidly from rootstock); iv) they produce chemicals that inhibit the seed germination and/or seedling growth of other plant species (allelopathy); and v) they may also produce chemicals that are toxic to potential seed-dispersing animals. Reports of the toxicity of invasive exotic plants to cattle are common, and such plants are probably also toxic to wildlife. Some of the most widespread species are listed in **Table 2.2**.

Grasses, bracken fern (*Pteridium aquilinum*) and species of the family Asteraceae (Compositae) (e.g. *Chromolaena odorata* pictured here) are among the most ubiquitous of tropical weeds that are capable of suppressing natural forest regeneration.

Table 2.2. Dominant weeds capable of suppressing forest regeneration.

Species	Family	Habit	Origins	Invasive exotic	Allelopathic	Toxic to Ungulates	Notes
Dicranopteris linearis	Gleicheniaceae	Climbing fern	Asia, Africa Australasia, Pacific	—	Yes	Not known	Forms a 2-m-high thicket on bare degraded land. Not fire or shade tolerant.
Chromolaena spp.	Asteraceae (Compositae)	Herb or shrub	New World	West Africa, Asia, Australia	Yes	Yes	Syn. *Eupatorium* (Asteraceae (Compositae)). Wind-dispersed seeds.
Lantana camara	Verbenaceae	Prickly, scrambling shrub	New World	Central Africa, Australia, India, Southeast Asia, Pacific Islands	Yes	Yes	Introduced as ornamental. Bird-dispersed fruits, ornamental. poisonous to humans. Coppices well, resilient.
Leucaena leucocephala	Leguminosae	Small tree	Belize, Mexico	Pacific Islands, north Australia	Yes	Yes (in large doses)	Introduced for firewood, fodder and biomass production. Fire promotes seed germination.
Mikania micrantha	Asteraceae (Compositae)	Vine	New World	Nepal, India	Yes	No	Introduced for military camouflage. Wind-dispersed vine smothers trees. Threatens rhino and tiger habitat in Nepal.
Mimosa pigra	Leguminosae	Prickly shrub	New World	Africa, India, Southeast Asia, Australia, Pacific Islands	Yes	Not known	Introduced for riverbank stabilisation. Accumulates dense seed banks. Thrives in wet areas and on disturbed soils.
Pteridium aquilinum	Dennstaedt-iaceae	Fern	Pan-tropical	—	Yes	Yes	Fire promoting. Fire resilient. Carcinogenic.
Grasses (e.g. *Imperata, Pennisetum, Andropogon, Panicum, Phragmites, Saccharum* and many species of other genera)	Poaceae	Herbs	Many	Many	Some species	No	Fire promoting. Fire resilient.

Predators of seedlings

In terms of biomass and species, insects are by far the most abundant herbivores, but in tropical forests, most insect species eat only one or a few plant species. Therefore, herbivorous insects are only capable of causing high mortality among seedlings growing close to the parent tree. This is because insects that are attracted to the parent trees also find and eat the seedlings growing beneath them (Coley & Barone, 1996). In deforested sites, however, small scattered seedlings are much harder to find, so herbivorous insects rarely limit forest regeneration.
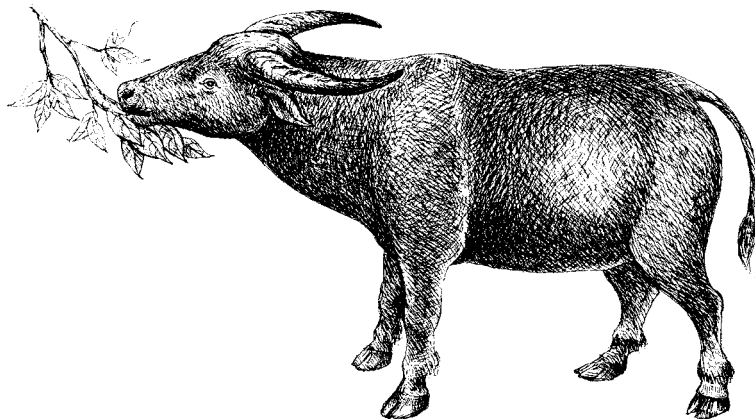
By contrast, large mammalian herbivores can have a serious impact on forest regeneration. Large wild herbivores, such as elephants, rhinos and wild cattle, are now so sparse that they rarely affect forest regeneration, except locally. Domestic cattle, on the other hand, are ubiquitous and they impede forest regeneration over large areas. In most tropical countries, it is common to find domestic livestock ranging freely across degraded forestlands. Their impact on forest regeneration depends on population density. A small herd of cattle might have no significant effect (or they might even be beneficial) but, where populations are dense, they can completely halt natural succession.

The most obvious impact of cattle is browsing on tree saplings. Cattle can be very selective, often eating the foliage of palatable tree species while ignoring that of unpalatable ones. Distasteful or thorny trees can thus become dominant, while edible ones are gradually eliminated. Cattle also trample young seedlings indiscriminately.

The potential beneficial effects of cattle include reducing competition for tree seedlings by grazing or browsing on weeds, although, as mentioned above, several of the typical weeds of deforested sites contain toxins that protect them against being eaten. Another potentially beneficial effect of cattle could be seed dispersal. Where large wild ungulates have been extirpated, domestic cattle can be the only animals present that are capable of dispersing large seeds from forest into gaps. Furthermore, their hoof prints can provide micro-sites for seed germination in which moisture and nutrients accumulate and weeds have been crushed.

The balance between these positive and negative effects and their relationship with herd density, site conditions and vegetation type are not fully understood. Therefore, further research is required to allow us to predict the overall effects of cattle on forest regeneration at any particular site.

Too many cattle can slowly devastate a forest by preventing regeneration, but they can also keep weeds in check and may act as seed dispersers.

Fire

Fires are a major constraint to forest regeneration. Infrequent, low-intensity fires may slow succession and alter the composition and structure of regenerating vegetation (Slik *et al.*, 2010; Barlow & Peres, 2007), but frequent burns can completely prevent it, leading to the persistence of grasslands where forests would otherwise grow.

Fires can occur naturally in all tropical forest types, even the wetter ones. In Amazonia, Borneo and Cameroon, layers of charcoal deposits deep in the soil profile show that rain forests have burnt at least periodically over the past few thousand years, at intervals of hundreds or thousands of years (Cochrane, 2003). Historically, such fires have been restricted to periods of severe droughts, but now, increased forest degradation, fragmentation and climate change are all contributing to increased fire frequency, even in the wet tropics (Slik *et al.*, 2010). The tree species of wet evergreen tropical forests usually have thin bark, making them highly vulnerable to fire damage. Even low-intensity fires in wet tropical forests result in high tree mortality and dramatic and rapid changes in tree species composition, especially where fires recur at short intervals (Barlow & Peres, 2007).

It is in the seasonally dry tropics where fires are the most prevalent threat to forest regeneration. By the end of the rainy season, weedy vegetation has often grown above head height and is practically impenetrable. In the hot season, this vegetation dies

Fire can burn in all types of tropical forest but is particularly frequent in seasonally dry forests.

back, dries out and becomes highly flammable. Each time it burns, most of the tree seedlings that may have gained a roothold amongst the weeds are killed, whereas the weeds and grasses survive, re-growing from rootstocks or seeds protected beneath the soil. Thus, the weedy vegetation creates conditions conducive to fire and in doing so prevents the establishment of trees that could shade out the weeds. Breaking this cycle is the key to restoring seasonally dry tropical forests.

Causes of fire

Fires can be started naturally by lightning strikes and volcanic eruptions. But, such natural fires are infrequent, allowing plenty of time in between each event for the trees to grow large enough to develop some resilience to burning. These days, however, most fires are started by humans. The most common reason for starting fires is to clear land for cultivation. The fires spread from cultivated land into surrounding areas, where they kill young trees, effectively halting forest regeneration. Fires are also used as a weapon in disputes over land tenure, to stimulate the growth of grasses for livestock and to attract wild animals for hunting. In addition to causing ecological damage, fires are a major health hazard. Smoke pollution causes respiratory, cardiovascular and eye problems in hundreds of thousands of people every year.

Human-caused fires are increasing throughout the tropics, both in frequency and intensity. The underlying cause is a growing human population that requires clearance of ever more agricultural land. This results in the fragmentation of forest areas, which exposes more forest edge into which fires can spread from surrounding areas. Within forests fragments, degradation creates more fire-prone conditions by opening up the forest canopy. This allows light-loving and highly flammable grasses and other weeds to invade and dead wood to accumulate. Furthermore, global climate change is resulting in hotter, drier conditions that favour fire in many tropical regions, particularly in the dry season.

Effects of fire on regeneration

Frequent fires reduce both the density and species richness of the tree seedling and sapling communities (Kodandapani *et al.*, 2008). Burning reduces the seed rain (by killing seed-producing trees) and the accumulation of viable seeds in the soil seed bank. It favours the establishment of wind-borne, light-demanding pioneer tree species at the expense of shade-tolerant climax species (Cochrane, 2003; Meng, 1997; Kafle, 1997). Fire burns off soil organic matter, leading to a reduction in the soil's moisture-holding capacity (the drier the soil, the less favourable it is for tree seed germination). It also reduces soil nutrients. Calcium, potassium and magnesium are lost as fine particles in smoke, while nitrogen, phosphorus and sulphur are lost as gases. By destroying vegetation cover, fire increases soil erosion. It also kills beneficial soil micro-organisms, especially mycorrhizal fungi and microbes that break down dead organic matter and recycle nutrients. Studies that have compared frequently burnt areas with those protected from fire show that preventing fires accelerates forest regeneration.

Fire and germination

Direct exposure to fire either kills the seeds of the vast majority of tropical tree species or significantly reduces their germination. Seeds lying on the soil surface are nearly all killed by even low-intensity fires, but those buried even a few centimetres below

the soil surface can usually survive (Fandey, 2009). The germination of a very small number of tree species can, however, be stimulated by fire. If burning disrupts the seed coat without killing the embryo, water entering the seed can trigger germination, and substances in smoke or from charred wood can sometimes stimulate germination chemically. Species whose germination can be stimulated by fire include teak (*Tectona grandis*) and some leguminous trees in dry tropical forests (Singh & Raizada, 2010).

Does fire kill trees?

Small seedlings and saplings are usually killed by fire, but larger trees can survive occasional low-intensity fires (i.e. burns restricted to the leaf litter or ground vegetation). So how large does a tree have to grow before it can survive fire? Bark thickness, rather than overall growth rate, appears to be the key survival factor (Hoffman *et al*., 2009; Midgley *et al*., 2010). Larger trees have thicker bark, which insulates their vital vascular system (the cambium layer) from the heat of fires, so they survive better than smaller trees. As a rough guide, trees with bark thicker than 5 mm have a greater than 50% chance of survival after a low-intensity fire (Van Nieuwstadt & Sheil, 2005). To develop bark of this thickness, trees must grow to at least 23 cm diameter at breast height (dbh), which takes a minimum of 8–10 years. Therefore, it is likely that forest regeneration will be severely impeded where fires burn more frequently than once every 8 years. In general, the trees of wet evergreen forests have relatively thin bark, and are therefore more susceptible to fire damage than those of seasonally dry or dry deciduous forests (Slik *et al*., 2010).

Even if fire kills the above-ground parts of a tree, the roots may still survive, insulated from the heat by soil. Food reserves that are stored in the roots can then be mobilised to support the growth of re-sprouts (or coppices) from dormant buds near the root collar or stem (epicormic buds). Re-sprouting capability varies greatly among species and is more common among dry deciduous forest tree species than among evergreen tree species of wet forests. Usually, a tree must grow for at least a year before it can re-sprout. So, frequent fires also reduce the chances of forest regeneration from re-sprouting.

2.3 Climate change and restoration

Climate change severely threatens tropical forests, reducing the bioclimatically suitable area for certain species (Davis, 2012) and increasing the risk of large-scale forest 'dieback' in some areas (Nepstad, 2007). International negotiations to shift the global economy from carbon-dependence to carbon-neutrality have largely failed (but are continuing). The burning of fossil fuels and continued destruction of tropical forests both continue apace. So it seems inevitable that concentrations of carbon dioxide, methane and other greenhouse gases will continue to rise over the next few decades (IPCC, 2007).

The relationship between rising atmospheric concentrations of greenhouse gases and global warming is well established. Therefore, predictions of future warming depend on the future levels of greenhouse gas emissions, which in turn depend on human population size and economic activity. Computer models predict that, with moderate economic growth and rapid adoption of green technologies, surface air will warm by an average of 1.8°C (range 1.1–2.9°C) by the end of this century. But with rapid

economic growth and continued dependence on fossil fuels this 'best estimate' climbs to 4.0°C (range 2.4–6.4°C) (IPCC, 2007). What is absolutely clear is that urgent and extreme action is needed now to deal with unprecedented changes in the environment.

Rainfall patterns will also change, but there is less agreement amongst meteorologists on how. Atmospheric warming will result in greater evaporation from water bodies and soil, causing some areas to become more arid. In those areas, forest fires will become more frequent, adding even more carbon dioxide to the atmosphere. On the other hand, increased water vapour in the atmosphere must result in more rainfall overall, but changes in global air currents are uncertain, so there is disagreement about when and where extra rain will fall. The latest computer models predict that rainfall will increase over tropical Africa and Asia and decrease slightly over tropical South America (by +42, +73 and –4 mm per year, respectively, with 2°C warming; double these values with 4°C warming) (Zelazowski *et al.*, 2011). In the seasonal tropics, dry seasons will

Climate change is predicted to result in reduced rainfall in South America where, in years of severe drought such as 2005 and 2010, areas of the Amazon rain forest switch from being a carbon sink to being a carbon source.

most likely become drier and rainy seasons wetter. Most computer models predict an increase in rainfall in the summer monsoon season of South and Southeast Asia and East Africa (IPCC, 2007). Droughts may also cause tropical forests to emit more carbon dioxide than they absorb (because of tree deaths and fire), thus exacerbating the problem of greenhouse gas emissions (Lewis *et al.*, 2011)

These changes in global climate may alter both the distribution of forest types and the mechanisms of forest regeneration described above. Since the climax forest type depends on the climate, changes in temperature and rainfall will alter the climax forest type suited to any particular site. Achievement of the climax forest type is the ultimate goal of forest restoration, and so climate change will have profound consequences for the planning and execution of forest restoration projects (see **Section 4.2**). The latest models predict that areas in South America that currently have a climate that is capable of supporting wet tropical forests will contract substantially, whereas such areas will expand in Africa and Southeast Asia (Zelazowski *et al.*, 2011). In South America, former ever-wet rain forests may become seasonally dry forests or even savannas. By contrast, in Africa, and Southeast Asia, it is not likely that wet tropical forests will spread naturally into new wetter areas because of limited seed dispersal and the existing occupation and use of the land. Climate change will also affect the distribution of forest types on mountains. In drier areas, higher temperatures might allow dry forest types to spread higher up mountains[1], displacing evergreen forests, but where rainfall increases, evergreen forest could spread to lower elevations.

The effects of global warming on the mechanisms of forest regeneration will also be significant. Changes in the climate, especially in the seasons, will result in changes in the flowering and fruiting times of plants, as well as to the life cycles of their pollinators and seed dispersers. This could result in a 'de-coupling' of reproductive mechanisms e.g. flowers opening when their insect pollinators are not flying. On the other hand, wind pollination and seed dispersal could benefit from global warming because wind-gust speeds and the frequency of storms capable of uplifting even large wind-dispersed seeds will both increase. Germination and early seedling development are both highly sensitive to temperature and moisture levels and could also be particularly vulnerable to the spread of weeds, pests and diseases that are favoured by climate change.

An increase in wildfires, with all the associated impacts described above, seems inevitable, particularly in the predicted drier areas of South America. There, more frequent wildfires are expected to bring about "substantial changes in forest structure and composition, with cascading shifts in forest composition following each additional fire event" (Barlow & Peres, 2007).

Does nature need help?

Some people take the view that deforested sites should be left to recover naturally and that forest restoration is "unnecessary interference with nature". This view fails to recognise that the situation today in most large deforested areas is far from 'natural'. Humans have not merely destroyed the forest, we have also destroyed the natural mechanisms of forest regeneration. All of the barriers to forest regeneration described in this chapter are caused by humans. Hunting threatens seed dispersal by animals,

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[1] The upper limit of their preferred temperature will ascend, on average, about 100 m elevation for every 0.6°C increase in temperature.

most wildfires are anthropogenic in origin and humans introduced most of the invasive weeds that now prevent tree seedling establishment. Forest restoration is merely an attempt to remove or overcome these 'unnatural' barriers to forest regeneration.

Even under the most favourable circumstances, natural forest regeneration occurs slowly. In his definitive text, *The Tropical Rain Forest*, P. W. Richards (1996) comprehensively reviewed forest succession throughout the tropics. He concluded: "if the seral vegetation is left undisturbed, succession leads eventually to the restoration of forest similar to the climatic climax. This process … probably takes several centuries, even when the cleared area is only a short distance from intact forest."

Unprecedented rates of biodiversity loss and climate change require urgent action. Waiting centuries for forests to regenerate naturally is no longer an option if species that are on the verge of extinction are to be saved or if carbon storage by forests is to have any impact on climate change. Human-caused problems require human-made solutions … and forest restoration is one of them.

A degraded mountainous landscape. Watershed degradation, soil erosion and landslides threaten agriculture. Isolated remnant trees and forest fragments, clinging to the ridges, may yet provide seed for forest restoration, but without active restoration, this landscape, its wildlife and its communities have an impoverished future.