trees and prevents the formation of uniform thickets. Planting should take place over a long time span to create uneven-aged structures of different sizes.

Conclusions

Mountain forests provide goods and services that are vital for people's well-being throughout the globe. They are, however, notoriously difficult to manage: their special topographic and climatic features mean that they are highly susceptible to degradation. To sustain mountain forests, careful and sometimes very sophisticated silvicultural approaches are required.

Careful silvicultural practices alone, however, will not ensure a sustainable future for the mountain forests of the world. A silvicultural system might be biologically perfect, but totally inappropriate if it fails to take into account the wider social context. Moreover, attempts must be made to anticipate the effects of changes in human demand, economic constraints, and ecological changes, such as global climate warming. Existing silvicultural systems must then be refined accordingly, or new innovative systems developed. Approaches such as the mountain group selection system, and their use on a large scale, are quite recent. Testing the real merits of these systems on an operational scale is a challenge that forest managers and scientists will have to face.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Forest Operations under Mountainous Conditions. **Plantation Silviculture**: Multiple-use Silviculture in Temperate Plantation Forestry. **Silviculture**: Coppice Silviculture Practiced in Temperate Regions; Forest Rehabilitation; Silvicultural Systems. **Windbreaks and Shelterbelts**.

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Ecology and Silviculture of Tropical Wetland Forests

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Introduction

Tropical wetland forests comprise a highly diverse group of habitats scattered throughout the humid or coastal tropical regions of Africa, Asia, the Americas, and Australia. They include inland riverine and swamp forests and coastal mangroves. Depending on definition, the total area of tropical wetland forest is probably in the range $160–180 \times 10^6$ ha worldwide. The tree species of inland forests are often of poor quality as timber, and are difficult to extract: forest management and silviculture are therefore often rudimentary. Nevertheless, some trees, and many secondary products, are of economic value. Mangroves, or tidal forests, in contrast are often of high value, and may be intensively and efficiently managed for timber, as well as providing a range of other goods and services.

The defining character of a tropical wetland forest is that the soil in which the trees stand is submerged or waterlogged, either permanently or intermittently. Intermittent flooding may be seasonal, for months at a stretch or for shorter periods, with the forest sometimes reverting to virtually dry land conditions between inundations. In the case of coastal mangrove forests, flooding is tidal and typically occurs twice daily for hours at a time, with the soil remaining waterlogged between high tides.

The topology and hydrology of wetland forests profoundly affect their ecology and relationship with adjoining ecosystems. Basin forests, with net inflow of water into a depression, are net accumulators of silt, nutrients, and suspended organic matter. Forests fringing rivers may trap sediment, hence may also be net accumulators, or, depending on flow patterns and other factors, they may be net exporters. Tidal forests are exposed in addition to fluctuating salinity as well as to fluctuating water levels, and have special adaptations to cope with salt as well as with waterlogging.

Adaptations to the Wetland Environment

Waterlogged ecosystems present particular challenges to plants growing in them. The underground roots must acquire oxygen for respiration and eliminate carbon dioxide. In a normal soil, gas exchange presents few problems. The atmosphere comprises 20% O_2, and, since much of the soil volume consists of air space, rapid diffusion is possible. In contrast, diffusion of O_2 and CO_2 through water occurs at a fraction of the rate through air. Moreover, even at saturation the concentration of O_2 in water is low: in the richly organic waters of many wetland forests microbial action is likely to reduce it further, creating virtually anoxic conditions.

Wetland forest trees have therefore evolved adaptations to their waterlogged environment. The ratio of root-to-shoot biomass is often lower in wetland trees: relatively less of the tree structure is in the anoxic waterlogged soil, and underground roots are in general restricted to the upper, partially aerated layers of the soil. The relatively high stem density of some basin wetland forests, a response to poor soil aeration, may also result in a relatively increased stem surface area available for gas exchange. In many species, the roots themselves leave the main trunk well above ground (or water) level. Such aerial roots take many forms, and are often described as buttress or knee roots. They have numerous lenticels to allow gas exchange with the atmosphere, and spongy aerenchyma tissue to allow gas movement by diffusion within the root mass. The most striking forms of aerial or buttress root occur in mangrove trees, such as *Rhizophora* species, where the roots may separate from the trunk several meters above ground level (**Figure 1**). Freshwater wetland trees such as *Pterocarpus* (**Figure 2**), *Casuarina*, and *Myristica* produce similar aerial roots, and are sometimes known as freshwater mangrove.

Aerial roots supply adequate anchorage and support. The absorptive function of roots is carried out by the reduced underground components: as these lie close to the soil surface they benefit from close proximity to the leaf litter layer in which inorganic nutrients are released by microbial decomposition.

Figure 1 A mature mangrove (*Rhizophora*) with aerial roots (Merbok, Malaysia).

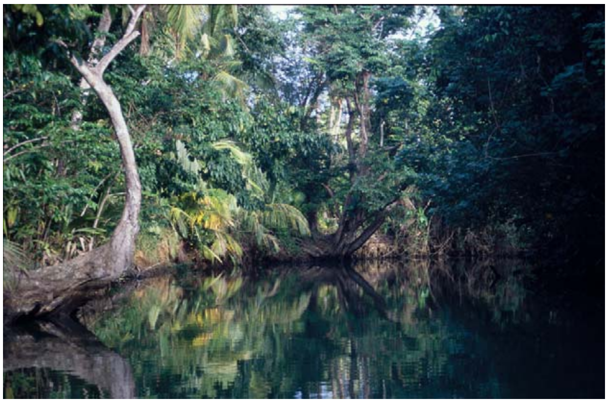

Figure 2 The bloodwood or freshwater mangrove, *Pterocarpus officinalis*, in Dominica. Photograph courtesy of Lance Leonhardt.

Mangroves (*Avicennia* and *Sonneratia* species) and some freshwater wetland trees (*Dactylocladus* in

Southeast Asia, *Mitragina* in Africa) facultatively produce another specialized respiratory structure, the pneumatophore. Pneumatophores are vertical peg-like columns of aerenchyma that grow from horizontal underground roots and protrude from the soil surface. One tree may be served by many thousands. In *Avicennia*, these are typically 10–15 cm in height, but in *Sonneratia* may be more than 3 m, suggesting that their role is to maintain contact with the atmosphere even at high tide, rather than merely to avoid anoxic soil.

Tidally inundated mangroves are also exposed to high and fluctuating salinity: significantly raised salinity also occurs in some other wetland forests in coastal plains. Several methods of coping with high salinity have evolved. The proximity of horizontal roots to the surface enables them selectively to exploit less saline water in the surface layers of soil, avoiding the sea water itself and the deeper soil water, which may be of higher salinity. In some mangrove species, such as *Aegiceras* and *Avicennia*, up to 90% of salt is excluded at the root surface, by a poorly understood selective physical process.

Inevitably, some salt does accompany water uptake. *Avicennia* and other mangrove species (*Rhizophora*, *Sonneratia*) tolerate high internal salt levels by sequestration within vacuoles and exclusion from cell cytoplasm. Finally, salt may be either deposited in bark or in senescent leaves that are then shed (*Xylocarpus*, *Excoecaria*) or actively secreted from leaf salt glands (*Avicennia*, *Aegiceras*, *Sonneratia*).

Reproduction in a flooded environment presents particular problems. Mangroves typically show vivipary, and the release of large floating propagules. Those of *Rhizophora*, for example, may be 0.5 m long (**Figure 3**). Flotation provides a means of dispersal, with the size and robustness of the propagule conferring resistance to current and wave damage, and its

Figure 3 Propagules of *Rhizophora*. Reprinted from Encyclopedia of Biodiversity, Vol. 3, P. Hogarth, Mangrove ecosystems, pp. 853–870, 2001, with permission from Elsevier.

advanced stage and the lack of a quiescent stage and the need to germinate enhancing its prospects of successful settlement. Freshwater wetland trees show fewer obvious reproductive adaptations, but the Central American *Pterocarpus officinalis* has a buoyant fruit 5 cm in diameter which can be dispersed by water currents.

Meaningful comparisons between wetland and dry tropical forests are not easy, and there are exceptions to all generalizations, but in general wetland forests are slower-growing and lower in above-ground biomass, and show simpler physical structure and reduced understorey vegetation. Tree species diversity is generally lower than in dry forests, decreasing with increasing frequency or duration of inundation: wetland forests have a tendency towards domination by a small number of tree species. In mangroves, and some fresh or brackish water coastal plain forests, there may be virtually monospecific zones within a forest. Offsetting relatively low tree species diversity, canopy epiphytes may be abundant. Riverine wetland forests tend to have greater productivity than those with stagnant water. Within the mangroves, increasing salinity is associated with lower growth rates and biomass, and towards the northern limits of mangrove distribution the combination of adverse physical circumstances results in dwarf forests, where the maximum height attained by mature trees may be as little as 1 m.

Wetland Forest Communities

The fauna of wetland forests falls into two more or less distinct categories: the terrestrial or arboreal, and the aquatic. Animals associated with the trunk, leaves, and canopy of wetland forests are in general similar to those in dry forests and other adjacent habitats. They are usually highly mobile, and individuals may move freely between the wetland forest and its surroundings. Most ground-living vertebrates such as deer, rodents, and lizards retreat from seasonal or tidal wetland forests as the water rises, and reenter as it falls: flying animals such as many bird, bat, and insect species can exploit wetland forests even when the ground is submerged, and may even benefit from the scarcity of predators.

Few species of bird, mammal, or insect are restricted to wetland forests: in Australia, for instance, of more than 200 species of passerine bird recorded from mangroves, only 14 are virtually confined to this habitat. The relatively small number of mangrove-specific bird species may reflect the simplified physical structure of the forest, with little scope for niche specialization. Similarly, although many monkey species forage within Southeast Asian mangrove forests, only the proboscis monkey (*Nasalis*) is found exclusively in mangroves and adjacent riverine forests. Among the invertebrates, many insect species occur in mangroves – any mangrove biologist can testify to the abundance of biting midges and mosquitoes – but only a single truly mangrove-specific species of ant has been reported, the Australian *Polyrachis sokolova*, which lives intertidally under the mud surface.

The aquatic components of wetland forest faunas are also largely the same as in adjoining habitats with few endemic species. In freshwater forests the dominant aquatic groups are mollusks (gastropod and bivalve mollusks) and fish. Mangrove faunas are dominated by marine fish and crustaceans. Among the fish, mudskippers are largely restricted to mangroves: the remaining species, often commuters, also occur in other habitats. The most abundant and diverse crustacea in Indo-Pacific mangroves are crabs, most notably fiddler crabs (*Uca*: family Ocypodidae) and leaf- or detritus-eating sesarmids (family Grapsidae). Fiddler crabs are deposit feeders, favoring sandy and muddy habitats which often coincide with mangroves. Sesarmids are more strongly associated with mangroves, at least in the Indo-Pacific region where some species have been recorded only from mangrove habitats: in the neotropics the association is less exclusive.

Freshwater forests are less well understood, but the general situation is likely to be similar to mangroves, with the majority of the forest fauna derived from adjacent terrestrial and aquatic habitats. The lack of a characteristic fauna does not, however, mean that the fauna is not important in the distinctive ecosystems of tropical wetland forests. In mangroves the role of sesarmid crabs, for example, is often crucial: by selectively predating seedlings, they influence the distribution of mangrove species, hence forest structure; by eating fallen leaves they facilitate energy flow through the ecosystem; by burying leaves they retain primary production locally; and by their labyrinthine burrows they aerate the soil and increase productivity of the trees. Fish that enter mangrove forests to forage at high tide represent a major channel of energy flow between mangroves and other habitats.

Similarly, in the freshwater forests of Amazonia, many species of fish seasonally occupy flooded forests. Amazonia has the most diverse freshwater fish fauna in the world: more than 1300 species have been described, and perhaps around 2500–3000 species exist, representing one of the most extreme cases of evolutionary radiation known. With the seasonal rise in river level, the adjacent forests are flooded for several months at a time, to a depth of up to 15 m. During this period many fish invade the forest. These range from predators such as piranhas (family Characidae) and small blood-sucking siluroid catfish to leaf-, fruit-, and seed-eating fish which have no clear ecological parallel elsewhere in the world. The characid *Colossoma macropomum*, for instance, has molar- and incisor-like teeth which have evolved to crush hard nuts. The gut of a single fish can contain up to 1 kg of seeds of the rubber tree *Seringa*, comprising a total of about 150 seeds. A single tree may carry only 100–200 seeds at a time. Many other fish species (including, despite their reputation, species of piranha) also eat seeds and fruit. Although it is hard to evaluate the importance of seed-eating fish, it is likely that, among other impacts, they contribute to the maintenance of tree diversity within the forest. They may also assist in seed dispersal.

Tropical wetland forests are therefore ecologically diverse, notwithstanding the common features of trees adapted to inundated habitats, and contain a fauna that comprises both aquatic and terrestrial components.

Silviculture and Management of Tropical Wetland Forests

Freshwater Wetland Forests

In the neotropics, wetland forests are often inaccessible for much of the year, and inhospitable because of the hosts of biting insects. Many of the tree species are of little commercial value, and the species richness that delights biologists means that, to foresters, the few economically valuable species tend to be sparsely distributed. Exploitation of neotropical wetland forests is generally minimal and management virtually nonexistent. Secondary forest products, such as fisheries, may be significant, but timber extraction is sporadic.

***Pterocarpus* forests** An example is the *Pterocarpus* forested wetlands of Central America and islands of the Caribbean (**Figure 2**). These are dominated by *P. officinalis* (Leguminosae), the bloodwood or dragon's blood tree. In coastal forests, for example in Puerto Rico, *Pterocarpus* forms monospecific stands, but it is more typical for it to comprise perhaps 70% of the basal area in a mixed forest which may contain scores, or even hundreds, of other tree species.

Pterocarpus is a species well adapted to the swamp environment. It grows to a height of 30 m, with buttress roots arising from up to 5 m above soil level. The subterranean roots are shallow, with nodules of symbiotic nitrogen-fixing bacteria, giving an advantage in a (presumably) nitrogen-depleted environment. A further, probably major, factor contributing to its dominance is the propensity to develop secondary sprouts (suckers) from the roots following damage or rotting of the primary trunk. This may enable reproduction in permanently flooded conditions, as the floating seeds of *Pterocarpus* cannot root in water deeper than 3–4 cm, but it is also highly advantageous in recovery following hurricane damage. Much of Central America and the Caribbean is subject to frequent hurricanes.

Unfortunately, given the relative abundance of the species, *Pterocarpus* wood is of poor quality, being weak, light (with a specific gravity of 0.3–0.6), and lacking resistance to termite and fungal attack. It is therefore of use chiefly for the manufacture of boxes and plywood, in the production of charcoal, and as fuelwood. More than 90% of the rural population of Central America depend on fuelwood for cooking. The blood-red resin that seeps out when the bark is damaged, and which gave the tree its common names, was formerly exported as an astringent and hemostatic, but is now of very limited pharmacological interest. Harvesting involves much waste, because *Pterocarpus* must be cut above the buttress roots: this further reduces its economic value.

Most attention is currently being given to enhancing the economic value of the swamp ecosystem so that *Pterocarpus* and other low-value species are replaced, where appropriate, by more valuable species. In Guyana and Surinam, for instance, swamp forests include the decay-resistant *Triplaris surinamensis,* the very hard *Eschweilera longipes* and *Ceiba pentandra*, and species of medicinal interest such as *Bonafousia tetratstachya*; other favored species in the region include *Symphonia globulifera*, *Calophyllum calaba*, *Carapa guianensis*, and *Virola surinamensis*.

In Guadeloupe, there are plans to cultivate *Calophyllum* and *Symphonia* at the expense of *Pterocarpus* where these species are already well established, to maintain monospecific *Pterocarpus* plantations where this species has virtual dominance, and to introduce, on an experimental basis, valuable nonnative species such as *Carapa* and *Virola*. Cultivation of economically desirable tree species will depend on successful harvesting and germination of seeds, and mastering effective planting techniques.

The Acai palm (*Euterpe*) One of the most successful manipulations of forest composition is of the multistemmed Acai palm *Euterpe oleracea* (**Figure 4**). This is widespread throughout parts of Latin America in *Pterocarpus* and other wetland forests, and is the source of several products of major economic importance. The fruits, of which a single tree produces about 20 kg per year, are used to produce a refreshing drink (acai) which is the most important nonwood product of the Amazon river delta, amounting to more than 100 000 t $year^{-1}$, valued at more than US$40 million.

Figure 4 The palm *Euterpe oleracea*, near Belem, Brazil. Photograph courtesy of Rolf Kyburz.

The other major *Euterpe* product is palm heart, a popular gourmet food in North America and Europe. In one region of Amazonian Brazil, harvesting of palm hearts employs 30 000 people and generates US$300 million annually. As the palm heart or ‘cabbage’ is the terminal bud of the palm, its removal kills the stem, and traditionally, Acai palm trees were simply cut down to harvest hearts. The relative ease of replanting in the middle of the forest and rapid growth, made this a reasonably viable process. A recent and more sustainable approach is to harvest stems from an individual palm by rotation, so new stems continually appear and a single tree can be cropped for decades. Regular cropping in this way also increases fruit yield.

Euterpe depends on the organic matter supplied by trees of the surrounding forest, so its successful cultivation depends on a balance being maintained with other species. Manipulation of wetland forest ecosystems, rather than single-species cultivation, can undoubtedly enhance the economic value of the forest resource. The success of this strategy depends on an understanding of the interactions between species. Due regard must also be had to other goods and services supplied by wetland forests, such as fishing, hunting, and ecotourism.

Mangroves

In contrast to the situation with freshwater wetland forests, mangrove forests are often intensively and efficiently exploited, using relatively sophisticated management strategies and techniques. This is particularly true in Asia, where large numbers of people depend directly or indirectly on mangrove forests. In addition to the use of mangrove wood as timber, fuelwood, and in charcoal production, mangrove leaves are used in fodder and medicinally, and the forests are the basis of local and nearshore finfish and shrimp fisheries and a productivity base for aquaculture; the protective value of mangroves against typhoons and coastal erosion generally is increasingly recognized.

There are many reasons why the exploitation and management of mangrove forests is so different from that of freshwater swamp forests. Mangroves almost always occur on the coast, or in the estuaries of large rivers. They are thus intrinsically more accessible than inland swamp forests. The number of species of mangrove tree is low: only around 50 true mangrove species are recognized worldwide, and an individual forest may be dominated by only two or three species. These generally grow in more or less single-specific zones, rather than being intermingled, so efficient extraction of a preferred species is relatively straightforward. And, finally, several mangrove species provide valuable timber which is resistant to insect attack and fungal decay.

An important factor in the management of mangrove forests is the typical mode of mangrove reproduction: vivipary, with the release of large, robust propagules. These can be collected either from the tree or after release, and either used directly or reared in nurseries for subsequent replanting (**Figure 5**).

The potential for ecosystem modification, and the effective management of the mangrove forest resource, is therefore greater than for freshwater forests. In countries such as Thailand and Malaysia, recognition of the economic importance has led to the development of long-term strategies for the sustainable management of mangrove forests, which in some cases have been in place for many decades.

Figure 5 Replanted mangrove, *Rhizophora mucronata* in the Indus delta, Pakistan (Korangi creek). The established trees are mixed *Avicennia marina* and *Rhizophora*.

The Matang forest, Malaysia One of the best examples of intense exploitation of a mangrove forest is that of the Matang forest of western peninsular Malaysia. The present sustainable management regime, accommodating timber extraction and other uses, has been running in more or less its present form for around a century.

The managed area of the Matang comprises an estuarine complex of streams, creeks, and inlets, amounting to more than 40 000 hectares. Around 2000 hectares are left untouched as virgin jungle reserve, a biodiversity reservoir which helps to sustain the surrounding managed area. Further patches are set aside for research, or protected as archeological, ecotourism, educational, or bird sanctuary forests.

The principal harvest from the Matang is wood for charcoal, the major domestic fuel of the local rural population. The management routine currently operates on the basis of a 30-year rotation period. The exploited forest is divided into blocks of a few hectares, allocated to charcoal companies by the Forestry Department, which manages the whole forest. Each block is clear-felled: workers move in by boat and demolish every tree with chainsaws, cutting the timber into logs of standard length. Where a cleared area abuts a river or tidal creek, a band of trees 3 m wide is left on the shoreward side of the block to prevent erosion of the bank. The logs are ferried to charcoal kilns in a nearby village.

No two adjacent blocks are cleared simultaneously, so that the forest is a mosaic of patches of different ages and newly cleared areas are always surrounded by mature trees. Spontaneous colonization and repopulation with incoming mangrove propagules are therefore rapid. The debris from the clearing operation takes about 2 years to decompose. A year after clearance, each site is inspected. If the area then covered by natural regeneration is less than 90%, repopulation is assisted by artificial planting, mainly with the dominant, and preferred, species *Rhizophora apiculata*. Local villagers rear seedlings in small nurseries for this purpose. At this time, weed species can also be removed by hand, or with weedkillers. The mangrove fern *Acrostichum* can be a particular problem (**Figure 6**). It is well adapted to occupying sunlit spaces in the forest, so rapidly occupies a cleared site, and prevents successful rooting of mangrove propagules. Destruction of seedlings by crabs and monkeys can also be a problem. The following year, the site is again inspected, and any parts where seedling survival has been less than 75% successful are again replanted.

Figure 6 *Rhizophora* in the intensively managed mangroves of Matang, Malaysia. All trees shown are of the same age, hence similar diameter. Much of the understorey vegetation is the mangrove fern *Acrostichum*, a significant weed species that may prevent the establishment of mangrove propagules.

Some 15 years later, the site is revisited, and the young trees thinned out to a distance of 1.2 m apart (based on a premetric distance of 4 feet, unchanged since). The thinnings – all the same age, hence a standard thickness – are valuable as fishing poles. When the stand is 20 years old, it is again thinned, this time to a distance between trees of 1.8 m (6 feet): this time the thinnings (still of uniform thickness) are of a size suitable for the construction of village houses. Because the previous thinning means that the trees are not crowded, these grow straight and are ideal for their purpose. Finally, after 30 years, the block is again clear-felled for charcoal.

Since management began, there has been a trend towards virtual monoculture of *Rhizophora apiculata* in the intensively managed areas of the Matang. During this time, there is some equivocal evidence of a slight decline in productivity, but overall the Matang is a model of sustainable management of a natural resource – a depressingly rare situation.

In 1992, wood extraction amounted to more than 450 000 t and was worth a little over US$4 300 000. In recent years, declining demand for charcoal, and a shortage of workers for the labor-intensive business of timber extraction and charcoal-burning suggest that the future value of the Matang may lie in other products. Although the management is largely directed towards timber extraction, this accounts for only around 12% of the total economic value. The area supports thriving fisheries: the offshore waters annually yield more than 50 000 tonnes of fish, valued at US$29 million, and supporting nearly 2000 people. Much of this probably depends on the productivity of the mangroves. Farming of the blood cockle (*Anadara*) currently runs at more than 34 000 tonnes a year, worth US$3 million, and could be further developed. The Matang also has considerable potential for tourism, being rich in wildlife, including otters, monitor lizards, and a wide range of birds, including the rare milky stork (*Mycteria cinerea*). At present, with virtually no infrastructure, tourism probably brings in around US$430 000 annually to the local economy.

Sustainable forest management is therefore of importance beyond the production of wood and other direct forest products. Even if the market for charcoal disappears, managed mangrove forests such as the Matang should therefore have good long-term prospects, provided the connections between mangrove production and other activities are fully recognized.

See also: **Plantation Silviculture**: Multiple-use Silviculture in Temperate Plantation Forestry; Sustainability of Forest Plantations. **Silviculture**: Managing for Tropical Non-timber Forest Products; Treatments in Tropical Silviculture. **Tropical Ecosystems**: Mangroves.

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