Hunter ML Jr (1990) *Wildlife, Forests and Forestry.* Englewood Cliffs, NJ: Prentice Hall.

Kelty MJ, Larson BC, and Oliver CD (eds) (1992) *The Ecology and Silviculture of Mixed-Species Forests: A Festschrift for David M. Smith*. Boston, MA: Kluwer Academic Publishers.

Oliver CD and Larson BC (1996) *Forest Stand Dynamics*, updated edn. New York: John Wiley.

Oliver CD and O'Hara KL (2003) Effects of restoration at the stand level. In: JA Stanturf and P Marsden (eds) *Restoration of Boreal and Temperate Forests*. Boca Raton, FL: CRC Press.

Smith DM, Larson BC, Kelty MJ, and Ashton PMS (1997) *The Practice of Silviculture*. New York: John Wiley.

Natural Regeneration of Tropical Rain Forests

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Introduction

Natural regeneration is the process by which juvenile plants and coppice that have established naturally replace plants which have died or have been killed. Over time, following a disturbance, the growth of natural regeneration will reestablish canopy trees. This natural recovery process can be exploited in tropical forest management systems to create a new stand after canopy trees have been harvested. This article provides a review of the advantages and problems associated with natural regeneration. The effects of different silvicultural systems on natural regeneration are examined and the causes of success and failure discussed.

Advantages and Disadvantages of Natural Regeneration

Tropical rainforests are well-known for their extraordinarily high diversity of species, including trees. The use of natural regeneration in forest management helps to reduce logging impacts on biodiversity, since the objective is to ensure that exploited trees are replaced by juveniles of tree species characteristic of the natural forest. The diversity of natural regeneration will generally exceed the diversity of species that could be planted on a commercial scale. For example, in a recent large-scale forest rehabilitation project in Borneo many thousands of hectares of logged rainforest were replanted with only 33 commercial tree species. Some of these were not native to the region. Planting replacement trees in sites that are often remote and inaccessible is an expensive operation. Consequently there is little incentive to use species that are of low commercial value or that are relatively slow-growing. Such species are only likely to remain a component of a sustainably managed forest under a natural regeneration system.

Natural regeneration systems exploit existing seed and seedling banks and circumvent the problem of obtaining healthy planting stock. Seed production in many important tropical tree species is erratic and poorly documented and it is often difficult or impossible to obtain a regular supply. Planting stock cannot therefore be produced on demand. Where planting stock is available it is often collected from a narrow range of sites outside the local area and is likely to be of unknown but probably rather narrow genetic composition. Planted seedlings often suffer an initial period of poor growth and high mortality, termed planting shock. Poor initial growth will often put planted trees at a significant competitive disadvantage relative to the regeneration of other plants in disturbed forest sites. In contrast, natural regeneration will often show enhanced survival and vigorous growth in response to canopy disturbance.

In many parts of the world little is known about the ecology of commercially important tree species, including their tolerance of a range of site conditions or their requirements for successful establishment as seedlings. This can make artificial regeneration problematic. Where new trees have been planted extensively in tropical rainforest (typically, enrichment planting of forests with poor natural regeneration of commercially valuable species), seedling mortality has often been high and growth rates disappointing. This has been attributed to poor site–species matching, poor planting and maintenance techniques. The use of natural regeneration increases the chance that seedlings and saplings are of species capable of growing to maturity under local site conditions because they belong to species (and ecotypes) that are already growing in the immediate vicinity.

Under an appropriate silvicultural system the density of seedlings in a naturally regenerating tropical rainforest can be very high. Densities in excess of 75 000 seedlings ha^{-1} of commercial species have been recorded in forests in Borneo. This gives a broad base for the selection of the fastest-growing, best-formed individuals of the most desirable species. In contrast, the costs of replanting a forest are so great that the forester generally aims to make sure that a large proportion of all individuals survive and grow to maturity regardless of their quality. However, a major disadvantage of natural regeneration systems is that the forester has only indirect control over the composition of future forest stands. Although an aim of natural tropical rainforest silviculture is to increase the regeneration of commercially desirable species and enhance their growth, this is constrained by the species and genotypes that are present in the seed and seedling banks. Genetic improvement is unlikely to occur through natural regeneration systems and little or nothing is known about the relative performances of different provenances of climax tropical rainforest trees.

Concern has often been expressed that the 'creaming' or preferential felling of the largest trees or those with the best form from an area of natural tropical rainforest will leave only trees with undesirable genotypes in the forest. Natural regeneration offers a simple method for reducing the risk of such dysgenic selection. Most climax tropical rainforest tree species have populations which are composed of large numbers of seedlings and saplings and progressively fewer larger-sized trees. The largest commercial-sized trees will therefore constitute only a small fraction of the total population (**Figure 1**).

There is also a strong relationship between tree size and fecundity for many tropical trees. This implies that the largest trees are likely to have made a disproportionate contribution to the genetic structure of the seed and seedling bank. As a consequence, if the forest is well-stocked with natural regeneration, harvesting of only the largest individuals is unlikely to result in an immediate loss of genetic variation.

Environmental Control of Regeneration

Foresters and ecologists have been aware for centuries of the importance of forest canopy gaps in the regeneration dynamics of most tropical rain-

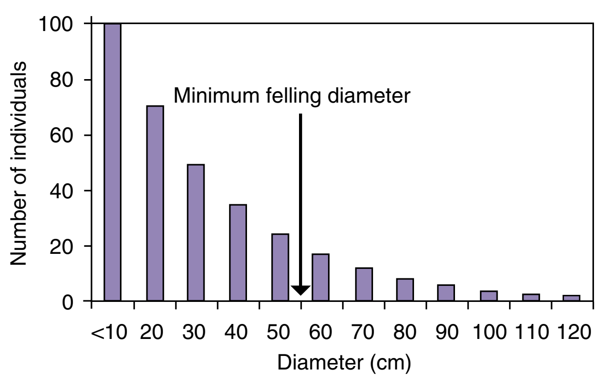

Figure 1 A typical size class distribution for a climax tropical rainforest tree species. Tree size is usually measured as the diameter of the trunk at 1.3 m above the ground.

forest trees. Gaps are formed naturally when canopy trees are damaged or die. They can range in size from a tiny patch of light formed by the loss of a branch to several hectares when many trees are lost in a landslide or major blow-down. Most seedlings require the enhanced light levels found in a gap in order to grow to maturity. Only the most shade-tolerant species can survive and grow in the deep shade of a forest understory.

Measurements of seed germination and rates of photosynthesis by seedlings have shown that species differ in their responses to increasing light levels. Two broad strategies have been described that characterize plant responses to disturbance. Pioneer species show significantly higher levels of seed germination under full sunlight. Their seeds are typically small, widely dispersed, and can remain dormant in the soil seed bank awaiting a disturbance to trigger germination. Once established, pioneer seedlings will grow very rapidly to maturity in a large gap, but they rarely persist for long in the shaded forest understory. In contrast, climax species have the greatest germination success in shade where their seedlings may persist for many years. Even relatively small increases in insolation will increase their growth and survival but they are unable to achieve the very high rates of growth of a pioneer species in the most disturbed conditions. Most species-rich, primary rainforests contain species which fall on a continuum of light response from the most shade-tolerant climax species to the most light-demanding pioneer.

The size of a canopy gap is the principal determinant of the amount and duration of insolation that penetrates the forest, hence different species of tree will find optimum radiation regimes for maximizing their growth in different sizes of gap. As a consequence, forests which are heavily or frequently disturbed will have abundant regeneration of light-demanding species. Pioneer species are often abundant in early successional forest communities such as those found on islands hit by tropical cyclones. Tropical rainforests which are infrequently disturbed are often dominated by more shade-tolerant, slow-growing climax species.

However, competitive superiority is not just determined by which plant has the greatest relative growth rate in response to the ambient light environment. Tall plants are able to capture more light and consequently grow faster and cast shade on the shorter plants beneath them. As the tallest plants in a gap may capture most incoming sunlight they will often dominate the regeneration regardless of their species. When the seedling bank and all advance regeneration is destroyed by a disturbance, the first plants to recolonize a gap will often preempt the light and delay or inhibit further colonization by other species. Furthermore, the species composition of seedling banks and the soil seed bank changes over time, reflecting the fruiting patterns of trees in the vicinity. Only a tiny fraction of the species found in a forest will be represented in the seed or seedling banks at any one place or time. A tree stands a good chance of regenerating if it is simply present as a seed or seedling when a gap forms, irrespective of whether it is well adapted to growing in that particular gap environment. It is salutary to note that in 1930 forest officers in Malaya concluded from practical experience that regeneration was influenced more by chance than by design and that regeneration of any particular species could not be relied on unless it was actually present before or immediately after the felling.

The implication of this for silvicultural systems that depend on natural regeneration is that it is crucial that the forest is already well stocked with abundant seedlings and advance regeneration of desirable species when the forest is logged. It is also important that logging does not destroy these seedlings. If this is not the case then regeneration will be composed primarily of noncommercial species or colonists.

Although many species of tropical rainforest tree have the ability to resprout after damage to the crown, coppicing has rarely, if ever, been used as a means to regenerate tropical rainforest after commercial exploitation. Resprouted stems are known to suffer much higher mortality rates than previously undamaged individuals and resprouts from large-diameter stems are more likely to die than those from small stems. Resprouting has also been found to be more common beneath small canopy gaps than in large ones. This implies that coppicing is unlikely to be a viable silvicultural system in tropical rainforests but may play an important role in forest regeneration after shifting cultivation.

Promoting Seedling Establishment

One of the real challenges in tropical rainforest management is to make sure that there is adequate regeneration before logging. In temperate forest silviculture this can be done by delaying felling operations so that they follow good seed years, by preparing suitable seed beds to enhance seedling establishment and thinning the forest canopy to encourage both seed production and seedling survival. Good seed years can be forecast when production forests consist of only one or a few tree species. However, in tropical rainforests it is much less easy to predict when or where a commercial species is likely to reproduce. Tree species fruit asynchronously in many tropical forests and their fecundity varies in response to very different climatic conditions. For example, the high-value tree Borneo ironwood (*Eusideroxylon zwageri*) has been noted for very poor regeneration for decades, to the point where, exacerbated by overexploitation, the species has become extremely rare. Recent extreme El Niño events which have caused high levels of seedling mortality in many other climax rainforest species seem to have promoted prolific regeneration of *E. zwageri*. Variation in the environment has different effects on the reproductive success of different species. The diversity of most tropical rainforest militates against efficient application of silvicultural treatments to increase the establishment of seedlings of desirable species to the whole forest block. Experience has shown that this only happens for the small number of species that produce abundant seed when the treatment occurs. Otherwise such treatments can promote dense regeneration of unwanted species that can inhibit the establishment of useful seedlings in the future.

The dipterocarp rainforests of South-East Asia are an important exception. Trees in the family Dipterocarpaceae occur in large numbers in these forests, and most provide valuable timber. A large number of dipterocarp species have supraannual, gregarious fruiting across large regions. As a consequence, at intervals varying typically between 3 and 11 years, there is substantial multispecies recruitment to the dipterocarp seedling bank. The density of seedlings can exceed several million ha^{-1} immediately after such a fruiting event, but declines rapidly with time until the next fruiting. These forests were some of the first tropical rainforests to be exploited extensively for timber. In the first half of the twentieth century regeneration of a forest was seen as one of the most important silvicultural tasks. There was a great deal of experimentation in dipterocarp rainforest, with methods for 'releasing' natural regeneration by thinning the canopy above newly established seedlings. A uniform shelterwood silvicultural system was developed that required the removal of all unwanted trees across the entire forest block, resulting in a drastic increase in understory light levels. An essential rule in this system was that felling should 'follow the seed,' meaning that a regeneration improvement felling could not be instigated until there was a substantial crop of newly established seedlings. The Malaysian Uniform System was found to result in a very large increase in the number of high-quality saplings of light-demanding dipterocarps. The success of the system was, however, attributable to the high density of adult trees of desirable species that simultaneously produced heavy seed crops. Similar tropical shelterwood systems, when applied in forests elsewhere in the humid tropics, have been considerably less successful. Either the systems proved too complex to apply reliably or, when applied indiscriminately to a whole forest block, resulted in dense regeneration of unwanted pioneer and light-demanding species.

Promoting Seedling Survival and Growth

Most tropical rainforests are now managed on a selection system, where no silvicultural operations are carried out at all. Some success has been achieved in improving the growth and survival of selected seedlings and saplings by opening the canopy directly above them and cutting back competitors. This type of treatment, known as liberation thinning, is relatively inexpensive and has been shown to increase the number of high-quality crop trees without impacting large areas of forest. Trees of unwanted species that are not impeding the growth of future crop trees are left alone. Concern has often been expressed that older saplings may become moribund and fail to respond to release. However, detailed long-term monitoring of advance regeneration has shown little evidence to endorse this concern. A positive relationship has been found between the height of advance regeneration and its growth response to artificial canopy gaps. Furthermore, it would appear that many canopy trees have experienced repeated periods of rapid growth interspersed with shade suppression in their passage to maturity.

Regrettably, as the costs of silviculture have increased, a view has developed among tropical foresters that logging alone would be sufficient to stimulate adequate regeneration and that silvicultural intervention is expensive and unnecessary. Extraction, rather than regeneration, has become the most important operation. Unlike lowland dipterocarp rainforest, many tropical rainforests have relatively low densities of commercially valuable species and sparse regeneration. Although selective logging has often stimulated vigorous regrowth, it has not been of valuable species. As a result of 'logging and leaving' there are now significant areas of secondary forest which have little or no productive potential. The only chance of rehabilitating such forests is through costly and unreliable enrichment planting. Many of these areas are now being converted to more productive nonforest uses, with serious consequences for conservation. An area of logged rainforest of more than 200 000 ha in the Ulu Segama area of Sabah, Malaysia, has recently been cleared and converted to pulpwood plantation because it was judged to be poorly stocked and devoid of natural regeneration and potential crop trees.

Why Does Natural Regeneration Fail?

Some of the most important causes of failure for natural regeneration include:

- Inadequate stocking of seedlings and saplings of desirable species at the time of harvesting. Many species of commercially valuable tropical rainforest tree do not have persistent seed or seedling banks. This is commonly true of more light-demanding climax species, including a number of important timber trees. In the Brazilian Amazon, species such as mahogany (*Swietenia macrophylla*) do produce seedling banks irregularly but these suffer very high rates of mortality in closed forest. Such species are problematic because the logging of large adults removes a significant proportion of the total population and the potential for future seed production. One possible solution is the retention of seed trees; however, experimental studies suggest that seed predation and poor germination limit successful seedling establishment in secondary forest. For many tropical rainforests the period during which recruitment can occur following a disturbance is short, because light and other resources are rapidly preempted by competing vegetation. Consequently the retention of seed trees is unlikely to result in regeneration of these species.
- Excessive damage to natural regeneration caused by harvesting operations. Surveys of logged tropical rainforest frequently report between 30% and 70% of the residual stand damaged. The majority of damage to natural regeneration is caused by careless and unplanned skidding rather than felling. Regeneration in badly damaged areas is either from the soil seed bank or from seed rain and is dominated by pioneer species. Some felling damage is inevitable when harvesting natural tropical rainforest but strict reduced-impact logging guidelines have shown that with care this can be substantially reduced.
- Poor maintenance of the forest following harvesting, resulting in poor growth and high mortality in existing seedlings. Scrambling bamboo and vines such as *Merremia* spp. can infest heavily damaged forest and smother young trees. Surveys in a logged forest in Borneo have shown over three-quarters of all trees to be infested with bamboo or vines. Little is yet known about the ecology of these climbers and the most effective methods for their control.

Long-Term Sustainability of Natural Regeneration

Sustainable use relies on the forest retaining its capacity to regenerate after harvesting. A very large proportion of tropical rainforest trees are dependent on animals for pollination and seed dispersal. Logging can disrupt animal communities in ways which have an impact on tree regeneration. Reduced pollination may lead to reduced seed-set or greater prevalence of inbreeding. Seeds which fall close to a parent tree are often found to suffer greater predation losses than those that are well dispersed. Similarly, seedling survival increases away from the pests and pathogens associated with a parent. Although there are indications that both pollination and dispersal may limit regeneration in forest fragments, there is as yet no clear evidence of impacts on seedling populations in large-production forests. However, seed predation rates have been found to be sufficiently high in logged forest to prevent regeneration of some tree species. Logging removes a significant proportion of the large seed-producing adults of commercial species and the residual seed trees become the focus of all predation.

Fire is becoming an increasing problem in many logged tropical rainforests and has a particularly severe impact on seedling populations. Almost no climax rainforest tree species have fire-tolerant seedlings and even lightly burned forests have been shown to be devoid of natural regeneration of anything other than pioneer species.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Silviculture**: Forest Dynamics; Forest Rehabilitation; Natural Stand Regeneration; Treatments in Tropical Silviculture. **Tropical Ecosystems**: Dipterocarps; Swietenia (American mahogany); Tropical Moist Forests,

Further Reading

de Graaf NR, Poels RLH, and van Rompaey RSAR (1999) Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. *Forest Ecology and Management* 124: 123–135.

Fox JED (1976) Constraints on the natural regeneration of tropical moist forest. *Forest Ecology and Management* 1: 37–65.

Hutchinson ID (1987) Improvement thinning in natural tropical forests: aspects and institutionalization. In: Mergen F and Vincent JR (eds) *Natural Management of Tropical Moist Forests – Silvicultural and Management Prospects of Sustained Utilization*, pp. 113–133. New Haven, Connecticut: Yale University, School of Forestry and Environmental Studies.

Kuusipalo J, Hadengganan S, Adjers G, and Sagala APS (1997) Effect of gap liberation on the performance and growth of dipterocarp trees in a logged-over rainforest. *Forest Ecology and Management* 92: 209–219.

Lowe RG (1978) Experience with the shelterwood system of regeneration in natural forest in Nigeria. *Forest Ecology and Management* 1(3): 193–212.

Nicholson DI (1979) *The Effects of Logging and Treatment on the Mixed Dipterocarp Forests of Southeast Asia*. Report FO: MISC/79/8. Rome: Food and Agriculture Organization of the United Nations.

Webb EL (1998) Gap-phase regeneration in selectively logged lowland swamp forest, northeastern Costa Rica. *Journal of Tropical Ecology* 14: 247–260.

Wyatt-Smith J (1963) *Manual of Malayan Silviculture for Inland Forests*. Malayan Forest Records No. 23. Kepong, Malaysia: Forest Research Institute Malaysia.

Managing for Tropical Non-timber Forest Products

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Introduction

Interest in the management of non-timber forest products (NTFPs) in the tropics has increased dramatically over the past 20 years. This process reflects observations that:

1. Some economically or culturally significant NTFP resources are being overexploited.
2. NTFPs can provide a raw material resource for local enterprise and income development.
3. NTFPs may be the only harvestable commodities left in degraded forests.
4. NTFPs have significant subsistence and cultural values to local peoples.

Although these concerns are most commonly associated with development forestry in the tropics, all of them are increasingly recognized as present and significant in temperate forests and rural economies (e.g., in the Pacific Northwest of the USA, Eastern Europe, and the UK).

Increasing interest in the poverty and development relevance of NTFPs has engendered work on the promotion of income generating enterprises based on them. Because this has a social focus much of this work has been undertaken by socially orientated advisors and hence on management systems based on participatory rural appraisal and other social science