AN EVOLUTIONARY PERSPECTIVE ON NATURAL DISTURBANCE AND LOGGING

Implications for Forest Management and Habitat Restoration

Colin A. Chapman and Robert A. Fimbel

Natural disturbances alter the structure and composition of tropical forests. The intensity and frequency of such events vary from daily limb and treefalls (Denslow 1980, 1987; Brown and Whitmore, 1992; Whitmore and Brown, 1996) to periodic large-scale disturbances, such as landslides, hurricanes, and fires that can damage hundreds of square kilometers (Garwood et al. 1979, Whitmore 1991). Recovery times from these perturbations may range from less than a year (e.g., limbfalls), to a number of centuries (e.g., after landslides that remove topsoil). Where geographical variations occur in the nature or extent of large forest disturbances, forest communities appear to have evolved to perpetuate themselves in the wake of such disturbances (Pickett and McDonnell 1989; Oliver and Larson 1990; Whitmore 1991, Perry and Amaranthus 1997). Silvicultural practices that mimic the local frequency and intensity of natural disturbance patterns have the potential to conserve large proportions of the evolutionarily adapted biodiversity found in dynamic tropical forest landscapes.

The aim of this chapter is to consider a conceptual framework linking the evolutionary and ecological processes of natural disturbance to management prescriptions for tropical forests (Whitmore 1991). The discussion begins by reviewing the concept that forest recovery following a disturbance event is a function of the evolutionary adaptations by the species in that area, local site conditions, and the intensity of the disturbance. Linkages between these factors and their influence on the type of forest community that might develop in an area are explored. The chapter closes with a discussion of how foresters can incorporate evolutionary and ecological information about a site into the development of silvicultural treatments—thereby somewhat *mimicking* the historical natural disturbance conditions that gave rise to the forest community in that area. Specific research recommendations on how to refine this process are noted.

An Overview of the Hierarchy of Factors Influencing Habitat Recovery

There are three hierarchical levels influencing forest recovery following a timber harvest: evolution, local environmental conditions, and modifications to the natural environment induced by the logging operation (see figure 22-1). Plant and animal communities experience a variety of natural disturbances that operate on different scales from isolated treefall gaps to hurricanes and landscape-level fires. The ability of rainforest plants and animals to recover from a disturbance event (natural or human-induced) is partially the result of natural selection that has operated in response to the disturbances a forest community has experienced over its evolutionary history (Skorupa and Kasenene 1984; Stocker 1985; Hartshorn 1989, 1990; Uhl et al. 1990; Whitmore 1991). Ecological conditions occurring at the local level temper this natural selection process, thereby influencing the speed of the recovery after a disturbance event. All other factors being equal, for example, a site located on poor soils will recover at a slower rate than a neighboring site on rich soils (Grubb 1995; Medina 1995). Finally, specific features of the logging operation will affect the recovery process (see chapter 2), with areas experiencing extensive logging road and skid trail networks recovering more slowly than areas with fewer disturbances of this kind (Sessions and Heinrich 1993a; Frumhoff 1995).

The importance of a forest's evolutionary history to its post-logging recovery should be emphasized. The rate of forest regeneration and the speed of recovery of wildlife populations vary greatly between sites, and this variation cannot be predicted based on the knowledge managers would typically have. The different evolutionary pressures operating in different forests probably account for some of the variability observed. An example of the recovery of primate populations following logging clearly illustrates the level of variability in how wildlife responds to logging. Blue monkeys (*Cercopithecus mitis*) have been classified as extreme generalists based on studies conducted in the Kibale National Park of Uganda (Johns and Skorupa 1987; Butynski 1990), and therefore should adapt relatively well to changes in their habitat following a

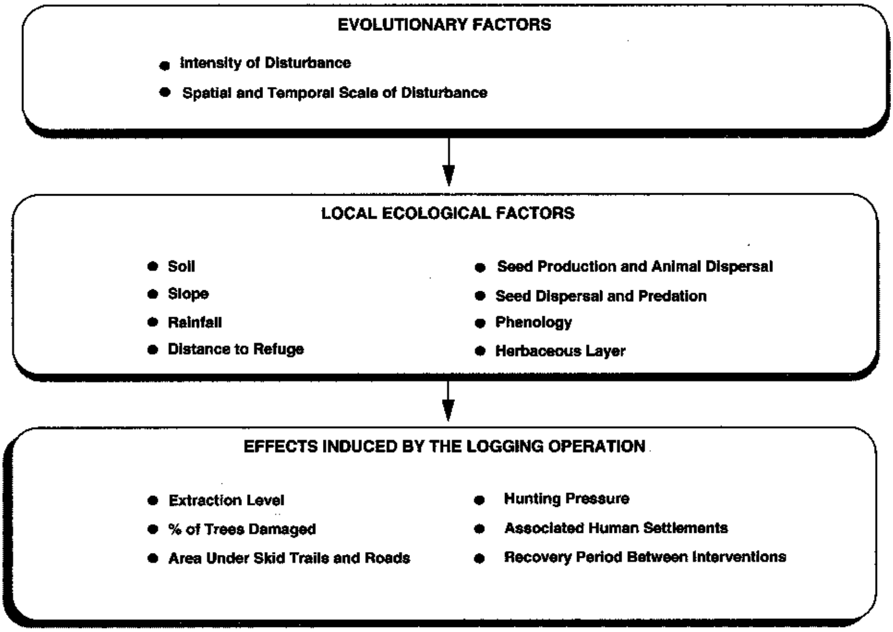


FIGURE 22-1 *Three hierarchical levels, and some of the factors within each level, influencing forest recovery following a timber harvest.*

disturbance such as logging. At the same site supporting this description, however, logging had a severe negative influence on this species (Skorupa 1988). Fifteen years after logging, logged areas had 20 to 30 percent fewer blue monkeys than unlogged areas (Skorupa 1988). Their populations continue to decline 28 years after the logging (C. Chapman, unpublished data). In contrast, blue monkeys in the Budongo Forest Reserve of Uganda are 3.7 times more abundant in logged areas than in unlogged areas (Plumptre and Reynolds 1994; see chapter 4).

Natural Disturbance Regimes and Their Influence on Forest Composition

Are there large-scale natural disturbance patterns that occur across continental or regional scales? Are there geographical variations in the frequency and nature of such disturbances? Do these conditions give rise to specific forest- and stand-types? The most complete evidence of geographical variation in large-scale disturbance events, and their subsequent influence on forest structure and composition, comes from the temperate zone (Oliver and Larson 1990; Barnes et al. 1998). As one example, the estimated recurrence interval between natural fires in North America (pre-European settlement) varied from two to 1,000 years (see table 4-1 in Oliver and Larson 1990). High fire frequencies usually give rise to forest-types dominated by fast-growing, early seed-producing, shade-intolerant species such as certain pines (e.g., *Pinus banksiana, P. rigida, P. taeda*), while low intervals of fire recurrence tend to support slower-growing, later-seed producing, shade-tolerant species such as sugar maple (*Acer saccharum*) and red spruce (*Picea rubens*). There are numerous exceptions to this simplistic cause-and-effect relationship, however, as a multitude of disturbance (wind, floods, erosion, siltation, landslides, etc.), topographic, edaphic (soils), and biotic (pests, competitors, mutualistic organisms, etc.) factors influence what species are capable of establishing and developing on a given site. Foresters are becoming increasingly aware of the multitude of variables shaping forest development, and continually seek ways to incorporate this knowledge into their silvicultural prescriptions (Kohn and Franklin 1997; Smith et al. 1997).

A similar suite of environmental variables determines the composition and structure of major tropical forest-types, and stands within them (Letouzey 1968,1985). Information on the natural disturbance regimes and the basic ecology of most tropical forest plants and animals is very limited, and often quite general. Broad regional assessments of natural disturbance events exist for the tropics (see box 22-1), however the high heterogeneity characterizing these large land areas permits only the most general insight into how tropical forests are likely to respond to timber harvesting practices. The ecology of most tropical species, including those exploited for timber, is also still largely unknown. There are exceptions to this rule. For a few select tropical tree species, information exists on their ecology, the forest communities in which they grow, and the forest management recommendations necessary to maintain them in a healthy and productive state (e.g., Greenhart [*Chlorocardium rodiei*] dominated tropical rain forest in Guyana—Steege et al. 1996; Ek 1997; Zagt 1997). Unfortunately, these examples are limited in number, and the skills necessary to implement them often lag far behind the research leading to these recommendations (see chapter 18).

Box 22-1 *Natural disturbance regimes at the continental and regional levels in the tropics, and their influence on forest composition.*

The most complete evidence of geographical variation in tropical forests comes from studies of seismic activity. Approximately 18 percent of tropical rain forests lie in zones of high seismic activity. This includes 38 percent of the Indo-Malayan forests, 14 percent of the South-Central American forests, and less than one percent of the African rain forests (Garwood et al. 1979). In American and Indo-Malayan forests, the effects of earthquakes can be dramatic. In 1976, for example, two earthquakes struck off the coast of Panama triggering extensive landslides that affected at least 450 km^2 of forested land and denuded approximately 54 km^2 (Garwood et al. 1979). In 1935, two similar earthquakes hit Papua New Guinea and denuded 130 km^2 of forested land (Garwood et al. 1979; Johns 1986d, 1992b).

Hurricane and cyclone activities also vary geographically. Hurricanes cause frequent natural disturbances affecting Atlantic coastal areas from northern South America, through the Caribbean and Gulf Coast region, to eastern North America (Boose et al. 1994). Between 1871 and 1964, an average of 4.6 hurricanes affected the Caribbean each year, with hurricanes hitting select areas once every 15 to 22 years (Tanner et al. 1991; Walker et al. 1991b). Between 1920 and 1972, 362 cyclones hit Madagascar (Ganzhorn 1995). The effect of hurricanes and cyclones on forest systems can be dramatic. When Hurricane Joan touched land in Nicaragua, for example, 80 percent of the trees were felled (Boucher 1990). African forests do not appear to be similarly influenced by cyclones or hurricanes.

Outside hurricane and cyclone belts, large windthrows can be common. Large windthrows have been reported from South America (Dyer 1988), southeast Asia (Whitmore 1984), and Africa (Thomas 1991b). Windthrows ranging in size from 30 to 3,370 ha have been documented, as widespread occurrences in mature Amazonian forest (Nelson et al. 1994).

Rivers often play large roles in changing forest dynamics in tropical forest areas with flat topography (Foster et al. 1986). In the Amazon basin, for example, 26 percent of the forest has characteristics of recent erosional and depositional activity caused by changes in the paths of water courses (Salo et al. 1986; Salo and Kalliola 1990).

There has been a great deal of debate over the historical frequency and extent of large-scale fires in moist tropical forests. Leighton and Wirawan (1986) reported on fires in southeast Asia that damaged 3.7 million ha, and suggested that massive die-offs from drought and fire occur in East Kalimantan once every several hundred years. Sanford et al. (1985) discovered that charcoal was common in the soils of mature Amazonian rain forest, and that these forests have repeatedly experienced fires over the last 6000 years. Based on charcoal deposits, Hart et al. (1997) describe that fires were relatively common but small (i.e., less than 1 ha) in the Northeast Democratic Republic of Congo starting 4,000 years ago. Hart et al. (1997) attributes the greater frequency of fires during the last two millennia to increased human activity. While conclusive evidence is lacking, and the role of human activity in initiating fires remains unclear, it appears that large-scale natural fires in moist tropical forests are more common in South America (Bush and Colinvaux 1994) and southeast Asia (Whitmore 1984) than in Africa (Tutin et al. 1996).

Continental and broad regional assessments permit only the most general insights into how tropical forests are likely to respond to timber-harvesting practices, owing to the very heterogeneous conditions characterizing these large land masses. Following the framework outlined earlier, investigations are best focused on a smaller spatial scale (e.g., forest type and stand levels) if efforts to reduce habitat disturbance and expedite forest recovery following logging are to succeed. One must always keep in mind, however, that the processes operating at a higher level may constrain what happens at a lower level.

The Hierarchical Concept and Silvicultural Refinement

There are a variety of studies that detail how the extraction level (Ward and Kanowski 1983; Wilkie et al. 1992) and road and skid trail design (Sessions and Heinrich 1993a; Frumhoff 1995) influence forest structure, composition, and rates of recovery in forests after logging (see table 22-1).

The interactive nature and extent of variability in these factors make it difficult to construct predictive recovery models. This is not to suggest that nothing can be done to expedite the postharvest recovery of logged forests. Techniques exist to minimize disturbances to forest structure, composition, and ecological processes during logging operations, thereby facilitating the recovery process (Pancel 1993; Pinard et al. 1995; Pinard and Putz 1996; part 5 of this volume). Many of these recommendations are also well known to foresters and harvesters. Further research in this area is a lower immediate priority compared with identifying the means of implementing what is already known (Palmer 1975; Struhsaker 1997).

Where information is limited about the ecology of a forest, including its historic exposure to disturbance events, what *cues* can foresters take from the existing forest to help in designing silvicultural prescriptions that are likely to expedite the recovery of the treatment area after logging? To begin, the regeneration and growth cycles of plants (and the animals that use this habitat) appear to be compatible with the frequency and intensity of disturbance events (Grime 1977; Pickett and White 1985; Oliver and Larson 1990). Knowing this, foresters must access any available information on the shade-tolerance and growth rates of important commercial timber species. Diameter distributions from forest inventories should help to confirm suspected shade-tolerance levels for species in questions (i.e., reverse *j* distributions indicate rich, semi-deciduous forests of southeast Cameroon. The size and abundance of these species suggests that they became established under a canopy that was much more open than the near-closed conditions characterizing these forests today. Foresters should, therefore, consider refining silvicultural prescriptions to create the necessary conditions that these species have evolved to require for their establishment and growth. These might include small clearcuts, shelterwood cuts, or group selection cuts (Smith et al. 1997). This approach should not only help to re-establish the harvested stems, thereby maintaining the value of the forest by helping to prevent its conversion to other land uses (see chapter 20), but it should also create environmental conditions that other plants and wildlife in this forest type are preadapted to.

Box 22-2 *Treading lightly may not always be the best silvicultural prescription.*

Several semi-deciduous forest types dominate the forest of southeast Cameroon (Letouzey 1968, 1985). Selective timber harvesting is common in these forests, focusing on a few high-value mahoganies (*Entandrophragma* spp., *Guarea* spp., and *Pericopsis elata*; see box photo 22-1), and several lower-value species that occur in very high densities (*Triplochiton scleroxylon*, see box photo 22-2, and to a lesser extent *Terminalia superba*). Within these species, merchantable stems are selected based on a tree's minimum diameter (60–100 cm), bole quality, and accessibility.

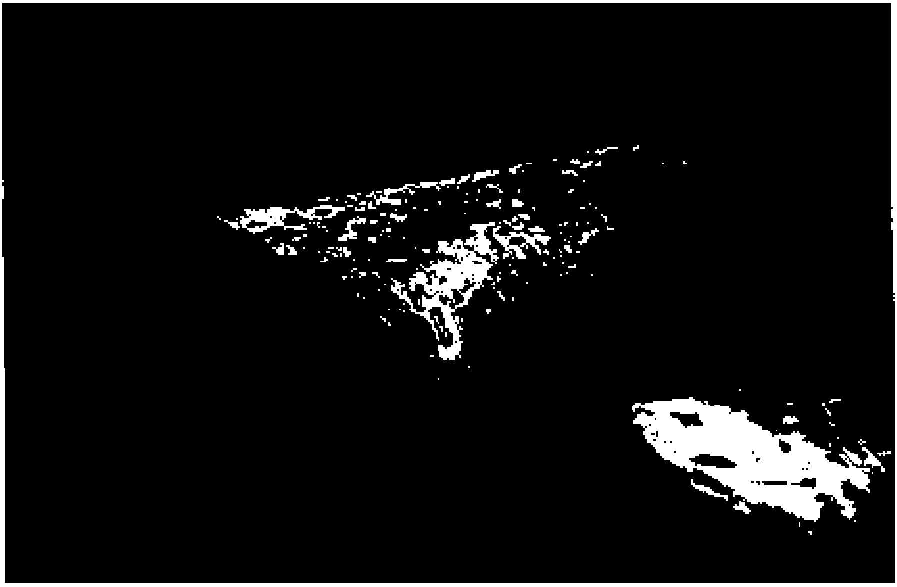
In 1995, 55 ha of upland forest were inventoried within a 400 km^2 area of unlogged forest (CTFT 1985; Fimbel et al. 1996, Fimbel and Runge, submitted). Extensive areas of forest appear to have established within the last 200 to 800 years, given the ecology of the forest dominants: *Albizia adianthifolia*, *Alstonia boonei*, *Ceiba pentandra*, *E. cylindricum*, *P. elata*, *T. superba*, *T. scleroxylon*, and others. These shade-intolerant, wind-dispersed species (Hall and Swaine 1981, Vivien and Faure 1985, Keay 1989, Hawthorne 1993), which currently lack representatives in their small-medium diameter classes (see box figure 22-1), must have been established at a time when shade conditions (i.e., forest basal area) were significantly lower than they are today. Regional diameter growth rates for the three most common canopy species—*T. scleroxylon*, *T. superba*, and *E. cylindricum* (which, combined, accounted for 24 percent of the recorded basal area)—suggest that the largest individuals of these species established 140 to 880 years BP (growth rates range from 1.3-13.8 mm/yr, n=1142; see Maitre and Hermeline 1985; API Dimako 1995). Radiocarbon-dated samples of *E. cylindricum* trees in northern Congo support these growth estimations. Thirty trees, ranging in diameter from 88 to 197 cm (in the survey, the largest individuals of this species approached 220 cm diameters), exhibited a mean age of 272 years (ages varied from 80 to 510 years, with low correlation between size and age of individual stems) (Fay 1997).

Current timber-harvesting prescriptions in this region call for selective cutting to remove all merchantable stems above the minimum allowable diameter limit. To date, impacts to the forest structure have been relatively limited, owing to forest planning (stocking surveys with subse-

TABLE 22-1 Select Factors Influencing Forest Habitat Recovery After Logging in Tropical Forests

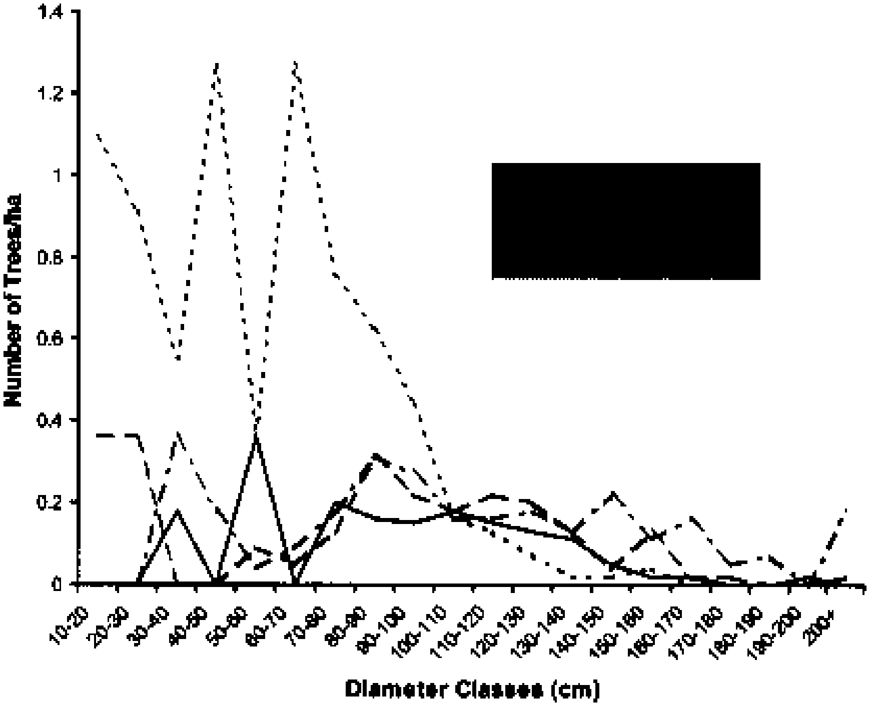
Factor	Reference
Soil fertility	Ewel 1980
Soil nutrients and pH	Jordon 1990; Grubb 1995; Medina 1995
Water stress associated with logging	Bazzaz 1990
Changes in mcorrhizae associated with timber extraction	Herrera et al. 1990
Nature and extent of skidding, soil compaction, and erosion following timber yarding	Uhl et al. 1982; Douglas et al. 1992; Cannon et al. 1994; chapters 2, 13, 14
Extent and rate of herb and shrub growth	Burgess 1975; Fitzgerald and Selden 1975; Brokaw 1983; Kasenene 1987; Yap et al. 1995
Extent of liana growth	Putz 1992
Proximity to undisturbed refugia and other seed sources	Viana 1990; Bierregaard et al. 1992; Marcot et al. (see chapter 3); Jansen and Zuidema (see chapter 23)
Availability of seeds (seedbank and seed rain) and seed dispersers	Fox 1976; Viana 1990; Whitmore 1991; chapters 3 -14
Ability of the trees to coppice	Whitmore 1991
Level of extraction and incidental damage	Uhl and Viera 1989; Wilkie et al. 1992; White 1994b; chapter 21
Death of damaged trees	Putz 1993; Putz and Chan 1986
Probability of fire inhibiting regeneration	Uhl et al. 1981; 1988c; Uhl and Buschbacher 1985; Janzen 1988; Woods 1989; Uhl and Kauffman 1990; Nepstad et al. 1991

shade tolerance, while distributions skewed towards a few large stems suggest shade intolerance). Growth rates usually have to be extrapolated from plantation trials or a few natural forest-monitoring sites (see box 22-2). These two variables, combined with the distribution of commercial stems across the forest (rare, clumped, and mono-dominant), should give a reasonable estimate of: a) when these trees established, and b) the intensity of the disturbance event that lead to their establishment. Large (100–200+ cm diameter) stems of the relatively shade-intolerant Ayous (*Triplochiton scleroxylon*), Sapelli (*Entandrophragma cylindricum*), Frake (*Terminala superba*), Kapok (*Ceiba pentandra*), and others (see box 22-2) dominate areas of the timber-



BOX PHOTO 22-1 One meter in diameter Iroko (*Pericopsis elata*) log awaiting log buyer in southeast Cameroon. (R. Fimbel)

BOX PHOTO 22-2 Large 2m dbh Ayous (*Triplochiton scleroxylon*) felled across main haul road in southeast Cameroon. (R. Fimbel)



BOX FIGURE 22-1 *Stems/ha, by diameter class, for four moderate- to shade-intolerant canopy tree species in the semideciduous forest of southeast Cameroon.*

quent road minimization), gradual slopes, low-to-moderate stocking of merchantable stems (mean of 3 to 4/ha), and limited pressure to convert the forest to other land uses (Fimbel et al. 1996). This approach appears to represent good forest management and the conservation of the forest resource, as most of the forest habitat remains intact. These conditions, however, may be relatively superficial. The majority of seed trees are being removed in the first and second cuts of this forest while creating small openings that are unsatisfactory seedbeds for the majority of commercial species harvested (Fimbel, personal observation). This approach amounts to little more than *mining* the forest resource. Continuing this silvicultural course is likely to lead to the long-term degradation of the timber resource (and habitat in general) as important commercial species fail to establish and recruit into the merchantable-size classes, thereby increasing the risk of forest conversion to more profitable land-use activities (e.g., oil palm plantations).

Foresters and conservationists would do well to look closely at what the prelogged forest composition and structure indicate about how these forests became established. The dominance of shade-intolerant species suggests that even-aged silvicultural prescriptions, while initially higher-impact than selection harvest-regeneration systems, may in the longterm be the most suitable management strategy for maintaining the diversity and productivity of these semideciduous forests. Time scales appropriate for the regeneration and recovery of these long-lived species must also be considered.

The above example is quite *coarse* in its approach, and foresters need to consider any other available information (soil properties, rainfall patterns, phenology, etc.) to help them in refining the size, shape, distribution, and frequency of their silvicultural interventions. Lacking extensive evolutionary or ecological information about a forest type, however, this approach does present an opportunity for resource managers to consider a wider range of silvicultural options than the selection cutting system that is applied with near uniformity across tropical production landscapes today.

On a cautionary note, foresters must keep in mind that while logging operations can be designed to mimic natural disturbance events, they cannot duplicate these conditions. Difficulties associated with seedling establishment in compacted soils on logging landings and skid trails, for example, are unique to logging with ground-based yarding (Pinard et al. 1996). Here the soil is compacted in a fashion that the flora (and fauna) is not equipped to combat (Whitmore 1991). Many of the trees damaged during the harvest also subsequently die, expanding the size and connectivity of gaps to sizes that are *atypical* in natural settings (Putz and Brokaw 1989; Cannon et al. 1994; see chapter 2). Putz and Chan (1986) documented that in an old-growth mangrove forest, all trees that suffered even slight mechanical damage die within a decade of being damaged. Logged areas in Uganda had up to 47 percent greater mortality than unlogged areas 30 years after logging (Chapman and Chapman 1997). Much work remains, therefore, in documenting the effects of timber-harvesting operations on forest structure and composition (see chapter 19), and refining silvicultural interventions to mitigate these environmental impacts (part V this volume), before prescriptions will exist that approach conditions characterizing natural disturbance events.

Research Recommendations to Promote Silvicultural Treatments That Mimic Natural Disturbances

There are a multitude of research studies needed to help minimize the environmental impacts associated with timber harvesting, while maintaining the economic bottom line of these operations (see other contributors to this volume). Where efforts are focused at refining silvicultural prescriptions so that they better mimic natural disturbance events and cycles, important areas for further research include the assessment of:

- Current and historic disturbance events that gave rise to present stand conditions; this includes the identification of disturbance type, intensity, frequency, and spatial impact across an area of forest
- How one disturbance event can predispose the forest to other disturbances. Logging or blow-downs, for example, can lead to increases in fuelloads that may predispose a forest to a catastrophic fire
- How the frequency of silvicultural interventions lead to a deviation from the natural forest recovery process; the arrangement of silvicultural treatments in the landscape over time is especially important for the maintenance of interior forest conditions
- Strategies used by species to survive disturbance events; this basic ecological information is critical to the perpetuation of commercial, threatened and endangered, and other species of interest in managed tropical landscapes
- Seasonal effects on the recovery process, including phenological conditions prior to and immediately after the logging event
- Techniques to assess how quickly the forest habitat and ecological processes recover after logging

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