

# Ecological knowledge of regeneration from seed in neotropical forest trees: Implications for natural forest management

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## Abstract

We discuss the main ecological factors that influence tree recruitment in neotropical moist- and wet forests within the context of timber management based on selective logging. We argue that setting aside protection areas in managed forests as a way to preserve ecological processes may not be sufficient to ensure sustainable levels of tree regeneration, and that a thorough understanding and application of tree seed ecology can help to refine management prescriptions. We review relevant aspects of tree reproductive biology, seed production and dispersal, spatial and temporal constraints on seed availability, disperser behavior, and the potential consequences of hunting and forest fragmentation on tree regeneration, and discuss their implications for biological sustainability in managed forests. Tree seed production can be influenced by the selective removal of neighbors of the same species (due to insufficient pollen transfer), flowering asynchrony, and attributes of the species' sexual system. The extent to which an area is supplied by seed can be affected by dispersal mechanism, spatio-temporal limitations to seed dispersal, and tree size-dependent levels of seed production at the species level. Studies of vertebrate-disperser behavior and tree seed deposition in logged forests are scarce and warrant further attention in order to refine our understanding of the dependency of sustained timber production on vertebrate fauna. Although much remains to be learned about tree seed ecology in neotropical logged forests, the baseline information presented here may offer a starting point for developing ecological criteria for seed tree retention. Furthermore, it may contribute in improving ecologically-based management prescriptions in order to enhance or at least maintain sufficient levels of natural regeneration without the need to rely on artificial regeneration. © 1998 Elsevier Science B.V. All rights reserved.

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“The major obstacle to improvements, and one of the driving forces behind the unabated decline of the tropical rainforest resource is not so much lack of knowledge but the failure to utilize effectively existing knowledge”. E.F. Bruenig (1996)

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## 1. Introduction

Guidelines for timber management in tropical forests (IUCN, 1992; Dykstra and Heinrich, 1996; Prabhu et al., 1996) require that at least some area(s) within management units are protected from intervention because of their fragility and ecological importance (e.g., steep slopes and riparian buffer zones) or

because they may serve as habitat refuges for pollinators and vertebrate seed dispersers. There is little empirical evidence to suggest, however, that tree regeneration will be maintained by simply setting aside conservation areas within logged forests. Forest managers need to ensure that processes contributing to tree regeneration also occur within the logged or otherwise silviculturally treated areas themselves if these areas are expected to provide sustained timber production. Enrichment planting (Weaver, 1987), and reduced-impact logging (Pinard and Putz, 1996; Johns et al., 1996) are thought to enhance or at least preserve stocking levels, but we argue that a thorough understanding of tree regeneration ecology, and how it may be affected by logging may also contribute to the development of biologically-sound management prescriptions. We recognize that this is not a new recommendation (e.g., Baur, 1964), but it is still poorly implemented in managed neotropical forests. Recently, Hammond et al. (1996) stressed the importance of incorporating tree dispersal ecology as a potentially critical tool for maintaining long-term forest productivity in managed Guianan forests. We hope that similar approaches will arise in the near future in other neotropical sites.

In this paper, we examine relevant ecological literature for neotropical forest trees in order to identify key factors that affect seed production and dispersal, and further discuss these factors within the ecological context of forests managed for timber. Due to their great biological potential for sustainable timber production, we focus on species-rich, moist and wet lowland forests in tropical America subjected to selective logging. Although the effects of logging on vegetation may be extremely variable and depend on pre-harvest conditions and harvesting methods used, we briefly describe some common structural characteristics of selectively-logged neotropical forests.

## 2. The post logging forest mosaic

Typically, logging in neotropical lowland forests is selective, and involves extraction of a few large individuals of commercial tree species over 20–50 year cutting cycles. Common harvesting intensities vary from less than 1 tree per hectare to 10 trees per hectare

(Graaf, 1986; Verissimo et al., 1992; Quirós and Finegan, 1994; Uhl et al., 1997). In most cases, forest management involves minimal labour investment beyond harvesting, but in others (although in a small proportion; Poore et al., 1989), pre- and post-harvest silvicultural treatments are implemented. Stand refinement (i.e., elimination of deformed, overmature, or non-commercial tree species), pre-harvest liana cutting, and removal of competitors of future crop trees via liberation thinning are the most widely used treatments (Graaf, 1986; Quirós and Finegan, 1994; Salick et al., 1995). For a more detailed description of these methods see Hutchinson (1988).

The canopies of moist and wet forests within the continental neotropics are temporally and spatially disrupted by localized treefall gaps that maintain about 10% of the forest area under open conditions at any time (Brokaw, 1985a; Sanford et al., 1986; Uhl et al., 1988). Other natural disturbances such as landslides, river meanders, and fire, also take place in these forests, but we do not consider them here as they do not directly relate to our discussion. In natural treefall gaps, soil disturbance occurs at a scale of meters (Putz, 1983; Ellison et al., 1993), and soil nutrient loss appears unimportant (Vitousek and Denslow, 1986; Uhl et al., 1988). The most dramatic shift in resource availability relates to changes in overhead light levels (Chazdon and Fetcher, 1984), with profound consequences for vegetation dynamics such as sapling release from suppression (Brokaw, 1985b; Uhl et al., 1988), increased levels of fruit production (Levey, 1988), and breaking of dormancy in soil-stored seeds (Garwood, 1989).

The extent of canopy opening in logged forests can be several times greater than in unmanaged stands (Jonkers, 1987; Uhl and Vieira, 1989; Verissimo et al., 1992) due to timber extraction and incidental tree mortality. Excessive canopy opening in felling gaps may increase fire susceptibility (Holdsworth and Uhl, 1997), retard tree regeneration due to vine competition (Putz, 1991), limit growth and survival of gap colonizers (Kennedy and Swaine, 1992), and reduce photosynthetic capacity of shade tolerant species due to photo-inhibition (Fetcher et al., 1996). The opening of logging roads, skid trails, and log yards generates distinct microhabitats that are also linked to high light levels, but these generally offer limited opportunities for tree establishment due to soil

compaction, high surface temperatures, and nutrient-poor substrates (Nussbaum et al., 1995; Pinard et al., 1996; Guariguata and Dupuy, 1997; but see Snook, 1993), all of which impede tree growth in the long term (Nicholson, 1965; Fox, 1976; Greacen and Sands, 1980). Because typical logging disturbances do not necessarily mimic natural disturbance regimes, much remains to be learned about tree regeneration in logged forests. However, by evaluating the main factors that affect tree recruitment in unmanaged stands, the potential implications of these factors for natural forest management can be discussed.

Regeneration requirements of neotropical lowland forest trees fall along a continuum based on a species' dependence on light for germination, establishment, and growth (Whitmore, 1989). At one end of the continuum, some tree species can only regenerate after seed germination is triggered by canopy and/or soil disruption, or if their seedlings benefit from high light environments for sustained growth. These species generally have animal or wind dispersed fruits, reach maturity at only moderate sizes, are relatively short-lived, and produce copious quantities of very small seeds. Clearly, recruitment of these 'pioneer' species in the logged mosaic is linked to felling gaps, landslides, and edges of roads and skid trails (Fox, 1976; Hawthorne, 1993; Pinard et al., 1996; Guariguata and Dupuy, 1997). At the other end of the continuum, tree species are able to germinate, establish, and grow under closed-canopy conditions and tend to have larger, animal- or gravity-dispersed fruits. We consider in this discussion only those long-lived heliophytic tree species whose seeds may germinate in either sunny or shaded conditions but whose seedlings require canopy openings to survive and develop into adults (primarily in the families Apocynaceae, Bignoniaceae, Leguminosae, and Meliaceae), and also shade tolerant tree species that are able to establish and mature in more shaded conditions.

### 3. Pollination and reproductive biology

In many neotropical forests, reproductive individuals of the same tree species are spatially isolated (Hubbell and Foster, 1983; Lieberman and Lieberman, 1994). Furthermore, most tree species are thought to be reproductively self-incompatible (Bawa, 1990).

These two attributes could make a given population prone to both losses in genetic variability and reductions in seed production after selective logging. Yet, generalizations about the genetic consequences of logging on the reproductive performance of neotropical forest trees remain for the most part, conjectural, because of lack of adequate information on effective population sizes (i.e., the fraction of the total number of individuals mating at any time) and gene flow distances. Although the degree of pollen transfer appears to be very high in low-density populations of tropical forest trees (Murawski, 1995), it is reasonable to expect that harvesting will affect the process of pollination and ultimately, may decrease seed production in those retained individuals as it has been shown by Murawski et al. (1994) in Sri Lanka. This hypothesis is also suggested by observations in Amazonian forests where one decade after logging, fruit production in matched samples of individual trees was lower in logged compared to unlogged forests (Johns, 1992). Indirect evidence also points out that removal of conspecifics during selective logging may also increase the degree of inbreeding in retained individuals. On Barro Colorado Island, Panama, Murawski and Hamrick (1991, 1992) reported for several tree species that elevated levels of self-pollination were associated with years of low numbers of flowering individuals. Similarly in the same area, diminished seed germinability (attributed to inbreeding) was evident in fragmented populations of the canopy tree *Spondias mombin* (Anacardiaceae), when compared to nearby populations from a larger forest tract (Nason et al., 1997). Clearly, logging has the potential effect of decreasing both the production and quality of tree seeds in the residual stand, but this aspect is largely understudied.

Maintaining adequate levels of seed production in dioecious tree species (i.e., those having distinct sexes on each tree) may be challenging in managed forests due to inadvertent removal of an excess of either male or female individuals. For example, Mack (1997) reported that seed crop size was negatively correlated with distance to the nearest male tree in *Aglaia* (Meliaceae) in an unmanaged forest in Papua New Guinea. Regardless of trunk diameter, those female individuals of *Aglaia* within 200 m of any male individual produced the largest seed crops. The implications of this study for generating criteria for seed tree

retention in dioecious species are important. If seed production depends on intersex distance, maximizing male density around female trees may be a reasonable practice to increase the potential for adequate regeneration.

#### 4. Phenology and seed production

Studies on tree phenology abound in the neotropical literature, but their application to forest management issues appear to be rare. It is well known that at the community level, seasonality in flower and fruit production is the rule in most neotropical wet and moist forests (e.g., Frankie et al., 1974; Foster, 1982; Carabias-Lillo and Guevara-Sada, 1985). At the species level, reproductive phenology varies from continual to supra-annual (Newstrom et al., 1994), while at the population level, reproductive output is highly variable due to fluctuations in the density of flowering individuals (Murawski and Hamrick, 1991; Hall et al., 1996). As a consequence, it is not uncommon that a few trees make up a disproportionately high contribution of the total seed crop and seedling recruitment in any given year (Schupp, 1990; De Steven, 1994; Forget, 1996, 1997a). This interannual variation has important implications for the retention of seed trees in managed forests. Adequate tree dispersion in space appears necessary to ensure seed supply if interannual variability in seed production is high for a given species, unless this is partially compensated by logging- and/or silviculturally mediated phenological changes. Few data appear to exist, however, on logging-related tree phenological shifts. At least in Old-World forests, evidence suggests that logging may enhance fruit production in smaller size classes (Appanah and Abdul Manaf, 1990; but see Thomas and Appanah (1995) for a critique to this study), and that soon after logging, trees adjacent to logging roads may produce more fruit than those within the forest (e.g., Johns, 1988). Although this effect is likely to be of limited duration as canopy closure proceeds, it may enhance immediate post-logging tree regeneration.

Potential effects of silvicultural practices on tree seed production remain unexplored for the most part. The application of liberation thinning as a way of releasing future crop trees from light competition may have an overall synergistic effect on tree performance

by accelerating its reproductive schedule. Pre-harvest liana cutting, carried out to reduce logging damage to residual vegetation or to liberate crop trees (Putz, 1991) may also promote fruit production of retained, liana-free individuals (e.g., Stevens, 1987). Carefully designed phenological studies seem justified to investigate how species-specific levels of fruit production may interact with tree size after stand manipulation (see Plumptre, 1995). Although information on tree size at the first reproduction is critical for maintaining adequate levels of natural regeneration in timber species, these kind of data appear to be very limited in the neotropics. In most cases, minimum cutting diameters are determined by market demands and political decisions, and not by a species' biology.

#### 5. Spatial constraints on seed availability

Seeds of tropical forest trees distribute in an uneven and restricted fashion around the parental source (possibly excluding species such as *Carapa*, *Prioria*, and *Mora*, that dominate flooded forests). Although maximum dispersal distances vary, strongly skewed seed 'shadows' are normal, whether propagules are wind- or animal-dispersed. For example, wind-dispersed tree seeds can travel >100 m from their source in undisturbed forest, but most (about 75%) fall within a 30 m radius from the parent (Augspurger, 1983; Augspurger and Hogan, 1983; Kitajima and Augspurger, 1989; Viana, 1990; Sinha and Davidar, 1992). Similarly, more than 90% of animal-dispersed tree seeds generally fall within a similarly small radius of their origin (Clark and Clark, 1984; Howe et al., 1985; Forget, 1992a, 1994) perhaps with the exception of mammal-dispersed, pioneer species such as *Cecropia* (Alvarez-Buylla and Martínez-Ramos, 1990; Medellín, 1994; see also Fragoso, 1997). At the community level, results from a seed-trap study in a 50 ha permanent plot on Barro Colorado Island, Panama, confirm the above: the majority of forest tree seeds are dispersed both in a temporally and spatially restricted fashion (Harms, 1997). Furthermore, weekly examination of seed contents of 200 traps over an 8 year period showed that seed dispersal of most tree species is spatially limited because only a small number of seeds reached more than a few traps; not surprisingly, the probability of any trap receiving seeds of a given

species generally fell as the distance to the nearest adult tree of that species increased.

A limited number of studies, however, include management recommendations based on empirical data from spatial, seed dispersal patterns. For secondary stands in Brazil dominated by the wind-dispersed tree, *Vochysia maxima* (Vochysiaceae), Viana (1990) suggests a minimum of 1.5 reproductive trees per hectare based on measured seed 'shadows'. Although for most tree species, the number of individuals that theoretically should be retained per unit area to guarantee broad seed coverage depends on information on their means of dispersal, individual size, and tree diameter at first reproduction, a reasonable minimum is perhaps 3–4 seed trees per hectare. Clearly, these estimates are rather unrealistic because the density of reproductively mature conspecifics of most tree species are much lower in many neotropical forests (e.g., Hubbell and Foster, 1983; Lieberman and Lieberman, 1994). Therefore, it appears that spatial constraints to seed dispersal is a fact that forest managers must accept, and that maximizing seed input for a given species may be in most cases, difficult to fulfil in practical terms. In fact, restricted coverage of seed distributions is argued as one mechanism that explains species coexistence in species-rich, tropical forests (Hurt and Pacala, 1995). If the management objective is however, to favor a group of species with similar regeneration requirements, maintaining adequate numbers of seed trees of each focal group of species (rather than individual species) may prove more feasible.

Other aspects related to spatial criteria for seed tree retention should also be considered. For example, seed trees retained near the edge of gaps have a higher risk of mortality than seed trees retained away from gap edges because of structural instability, either due to an inability to sustain its own weight when neighbors are removed (Holbrook and Putz, 1989), or to the development of excessive crown asymmetry (Young and Hubbell, 1991; Young and Perkocho, 1994). However, there are instances where retaining a seed tree at gap edges may be justified. In lightly-logged ( $2\text{--}10\text{ m}^3\text{ ha}^{-1}$ ), seasonally dry tropical forest in Lomerío, Bolivia, seedlings of commercial species such as *Astronium urundeuva* (Anacardiaceae), *Anadenanthera colubrina* and *Centrolobium microchaete* (Leguminosae), and *Cedrela fissilis* (Meliaceae), are

found almost exclusively in canopy gaps (Guzmán, 1997). However, most of their seed trees are surrounded by closed forest, where seedlings of these species are notably lacking (Pinard, unpublished data). Thus, at least for heliophytic species, retention of seed trees near edges of gaps may be necessary to increase the likelihood of seeds falling onto a substrate suitable for seedling establishment.

Biological constraints for the assurance of adequate seed coverage may be partially overcome by considering morphological and abiotic factors that may influence a tree's seed crop. It is well known that attributes such as trunk size and form, and crown illumination index (Dawkins and Field, 1978) are commonly applied as qualitative predictors of seed crop quality (e.g., Magalhaes, 1982). Also in most cases, diameter at breast height (d.b.h.) is positively linked to crop size (e.g., Sarukhán, 1980, Leighton and Leighton, 1982, Peters, 1990, Chapman et al., 1992). However, average seed size can vary substantially among conspecifics of comparable d.b.h. Howe and Richter (1982) found in a population of 46 trees of *Virola surinamensis* (Myristicaceae) in Panama, that minor differences in seed mass resulted in considerable variation in seedling dry matter accumulation. Larger seeds can still retain their germination capacity if some tissue is lost (Denslow, 1980; Harms and Dalling, 1997), and larger seedlings may show higher survival rates than smaller ones (De Steven, 1994). Another case study is worth mentioning. In production forests dominated by *Carapa nicaraguensis* (Meliaceae) in Northern Costa Rica, minimum d.b.h. at reproduction of this species is  $\approx 40$  cm and maximum d.b.h. is  $\approx 2$  m (McHargue and Hartshorn, 1983), but 50% of the total seed production on an area basis comes from the 40–60 cm d.b.h. class. This is partly because smaller individuals of shade tolerant tree species are more abundant than larger ones. However, the smallest size classes produced the heaviest (dry weight) seeds and seedlings (Peralta, unpublished data). Although the long-term advantage of these early differences in seedling vigor remain to be determined, these observations warrant further attention for a multitude of neotropical forest tree species. Because the largest individuals may not necessarily be the best seed trees, the uniform application of qualitative predictors of a tree's seed crop should not be used as a prescription for all species.

## 6. Post-dispersal fate of seeds and seedlings

Survival of recently dispersed seeds and emerging seedlings depends to a large extent on their post-dispersal density and distance from the parent plant, two variables which are usually inversely correlated. For example, Clark and Clark (1984) reviewed 24 data sets on tropical forest woody plants and showed that most studies found either density-dependence or distance dependence effects in progeny mortality (see also Hubbell et al., 1990; Condit et al., 1992). Predator satiation close to the parent tree (e.g., Forget, 1992b), and both density- and habitat-dependent pathogen attack may be partly responsible for this spatial structuring (e.g., Augspurger, 1984; Augspurger and Kelly, 1984; Gilbert et al., 1994).

Seed predation is a major constraint for tree regeneration in neotropical forests, but levels can vary dramatically among tree species (e.g., Terborgh et al., 1993; Chapman and Chapman, 1996), as well as among years for a single species (e.g., Schupp, 1990). Moreover, levels of seed predation may be influenced by forest habitat. In Central America, Schupp (1988) and Schupp and Frost (1989) showed that for a given species, seed and seedling predation can be disproportionately higher in treefall gaps than under adjacent closed canopy, probably due to a high abundance of rodents which preferentially forage in gaps (Forget, 1997b). In a comparison of levels of seed predation in two vertebrate-dispersed tree species in forest strips clearcut for timber in lowland Peru (Notman et al., 1996), predation in regenerating strips was significantly greater than around trees in intact forest for *Pouteria* sp. (Sapotaceae), while the opposite pattern was found in *Macoubea guianensis* (Apocynaceae); this variation in predation levels was probably related to species-specific differences in their seed consumers. The implications of these results for developing criteria for seed tree retention in vertebrate-dispersed species include a recognition that the importance of predation to tree regeneration is likely to vary by species and by habitat within logged forest.

## 7. Seed dispersal in logged forest

Most neotropical tree species with light-weight, wind-dispersed seeds rely almost exclusively on

canopy gaps or large disturbed areas for sustained growth (e.g., Augspurger, 1983, 1984; Snook, 1993). Wind-dispersed seeds tend to fall in higher numbers in canopy gaps than in the understory (Augspurger and Franson, 1988; Loiselle et al., 1996), because seed deposition in gaps is favored by local turbulence of air flow (Burrows, 1975). If harvesting changes wind patterns immediately above the tree canopy, logging may influence dispersal distances and depositional patterns in wind-dispersed tree species. Clearly, knowledge of prevalent wind direction and the distribution of felling gaps are important for developing guidelines for seed tree retention of wind-dispersed species (e.g., Stanley and Gretzinger, 1996; for *Swietenia macrophylla* [Meliaceae] in Guatemala).

Compared to wind-dispersed tree species, however, decisions about where to leave vertebrate-dispersed seed trees appears much more difficult because variability associated with disperser type (e.g., terrestrial, volant), fruit quality (i.e., caloric content), size of seed crop, and forest habitat structure, create a much more complex set of interactions governing the regeneration process. For a given tree species, seed dispersal by different frugivorous species can vary due to post-feeding habitat preferences, seed deposition patterns (i.e., clumped vs. scattered, close vs. away from the parent tree), and average direction of disperser movement. As an attempt to condense this variability into interpretable patterns, Schupp (1993) argues that the role of seed dispersal by animals may be quantified in terms of 'dispersal effectiveness' (or the contribution a disperser makes to the future reproduction of a plant), and defines it as the product of *quantitative* (e.g., number of disperser visits and/or number of seeds dispersed per visit) and *qualitative* (e.g., quality of seed processing, and/or quality of seed deposition patterns) components. Schupp also provides evidence that for a given plant species, not all dispersers share equal weights for each component. In particular, quality of seed deposition, or the probability that a deposited seed produces an adult individual (e.g., if recruitment is favored close or away from the parent source, in closed forest or in a gap), is a crucial component for evaluating dispersal effectiveness. Thus, quantifying dispersal efficiency for a given set of dispersers, may be used as a crude index for determining a tree species' 'best' disperser. This kind of data can be used for assessing conservation

priorities for wildlife in production forests. Moreover, manipulative studies that assess microhabitat suitability for seed survival (e.g., Schupp, 1988; Notman et al., 1996; Terborgh et al., 1993) may also be used as baseline information to develop rough guidelines for seed tree retention in vertebrate-dispersed species. There is a vast amount of both theoretical and empirical information on vertebrate seed dispersal in neotropical forests (e.g., Fleming and Estrada, 1993; Levey et al., 1994) and it would be worthwhile if some of this research were replicated in logged forests.

Selective logging is likely to influence seed dispersal by altering vertebrate abundance or by inducing changes in disperser behavior. For example, large canopy frugivores (primates and birds) may avoid recently created gaps and are unlikely to deposit seeds there (e.g., Forget and Sabatier, 1997). Avian frugivores constitute an important functional group for tree seed dispersal (Howe and Smallwood, 1982; Levey et al., 1994) and are sensitive to logging, although their sensitivity to habitat may vary according to species (Johns, 1991; Thiollay, 1992). Studies on seed dispersal by Gorchoff et al. (1993) revealed that many bird species failed to reach the center of a 30-m-wide clear-cut within old-growth forest. Management guidelines stress the importance of unlogged compartments as refugia for retaining the full complement of forest fauna, but this recommendation does not necessarily imply that the seed-dispersal function of at least the avian community will be maintained in nearby logged compartments. Further research is warranted on the functional relationship between unlogged and logged forest compartments for avian seed dispersal.

Changes in primate abundance on tree regeneration in logged forests also merits attention. Although seeds that are dispersed by primates can travel hundreds of meters away from their source in some neotropical forests (Estrada and Coates-Estrada, 1986; Julliot, 1996), dispersal by this group has been rated as relatively 'unimportant' for tree recruitment because large aggregations of (defecated) seeds and emerging seedlings (see Julliot, 1997) are prone to high density-dependent mortality (Howe, 1990). There is evidence, however, that monkeys may be effective dispersers by defecating seeds in sites that offer a high probability of survival (Forget and Sabatier, 1997). Whether potential reductions in abundance of frugivorous primates in logged forests are inconsequential for successful tree

regeneration remains an open question. Observations of logging impacts on primate populations appear to be lacking in the neotropics, but examples from other tropical locations suggest moderate resiliency. In Uganda, primate density was higher for two species in logged vs. unlogged sites, while three species showed no apparent difference (Plumptre and Reynolds, 1994). In Malaysia, logging destroyed primate travel routes through the canopy but populations were able to descend to lower layers with concomitant dietary adjustments (Johns, 1986). If research on the role of frugivorous primates reveals that they are important for tree recruitment, the implications for certain silvicultural treatments will need to be considered. For example, pre-felling liana cutting can be potentially detrimental both for primate populations and ultimately for the regeneration of monkey-dispersed tree species due to reduced access to other trees (Putz et al., in press).

## 8. Hunting and fragmentation

Hunting pressure can be high in logged forests (Bennett and Dahaban, 1995; Rumiz et al., in press), and the preferred game species are often large birds and mammals (Redford and Robinson, 1987; Redford, 1992; Bodmer, 1995) that act as important seed dispersers (Howe and Smallwood, 1982). There is growing evidence that for some species, tree recruitment in neotropical forests can be negatively influenced by changes in mammal assemblages due to hunting, spatial isolation, and fragmentation (Dirzo and Miranda, 1991; Leigh et al., 1993; see also Chapman and Chapman, 1995; but see Harrington et al., 1997). For example, hunting of large scatterhoarding rodents (e.g., *Dasyprocta* spp.) can be detrimental for the regeneration of some tree species because these animals bury their seeds, many of which are later undiscovered and left to germinate (Forget and Milleron, 1991). Forget (1994) found that although most (unburied) seeds below adult trees of *Vouacapoua americana* (Leguminosae) in French Guiana failed to establish within 8 months of dispersal, virtually all surviving seedlings arose from those seeds that were buried by scatterhoarding rodents.

Even if protected tracts of unmanaged forest are unable to maintain vertebrate dispersers that specialize

(*sensu* Howe, 1993) on a few tree species, potential loss of some of these species may be compensated for by others with similar function ('species redundancy'; Walker, 1992). Nevertheless, dispersal effectiveness may vary among dispersers as pointed out above. Although many timber species currently harvested in the neotropics have wind-dispersed seeds, an important number are also dispersed by mammals and birds (Martini et al., 1994; Hammond et al., 1996). Research on tree recruitment patterns in logged forests in relation to either absence of certain vertebrate dispersers or overabundance of vertebrate seed predators (e.g., Asquith et al., 1997) warrants further investigation.

## 9. Conclusions

In this review we have highlighted the main factors that influence recruitment in neotropical forest trees and discussed how they can be manipulated to enhance, or at least maintain, adequate levels of natural regeneration in forests managed for timber. Although biological constraints on the regeneration of tropical lowland forest trees undoubtedly exist, and have been cited as a major impediment to sustainable forest management (Wyatt-Smith, 1987), this is to some extent, a biased perception. For example, we believe that lack of effective communication between tropical forest ecologists and forest managers has often led the latter to a sometimes blind reliance on artificial regeneration prescriptions (e.g., line plantings) as the only possible way of achieving desired tree stocking levels. In some neotropical countries, implementing artificial tree regeneration in logged forests is even part of the forestry law and in some situations, these practices may prove detrimental to the forest structure and its biological diversity (Mason, 1996). Enrichment planting generally involves high costs in nursery maintenance and field labor, whereas developing silvicultural options that rely on a sound knowledge of tree regeneration plus low-intensity site preparation may prove more cost-effective. It should be pointed out, however, that most of the research cited in this review comes from protected forests, where the biotic and abiotic factors that influence tree regeneration may not be the same as those that operate in logged- or silviculturally-treated stands. Therefore, ecologists interested in natural forest management

need to be careful when applying models based on research done in unmanaged forests.

Research intensification on applied seed ecology can greatly complement current silvicultural knowledge in the neotropics. It is often argued that for practical reasons, timber management in highly diverse neotropical forests should aim at ecological guilds of tree species (based on their light preferences for establishment and sustained growth; e.g., Welden et al., 1991) rather than to single species (Panayotou and Ashton, 1992). This approach could benefit from concurrent research on seed ecology in order to strengthen silvicultural knowledge, as managing solely for guilds based on light preferences may ignore important differences between species. For example, Camacho and Finegan (1997) defined 5 guilds of tree species based on statistical clustering procedures of stem diameter increments (see Alder, 1995) in a forest managed for timber in northeastern Costa Rica. The fastest-growing guild in their sample grouped well-known light-demanding species, but with contrasting dispersal (and most likely regeneration) modes: *Croton smithianus* (Euphorbiaceae: explosively-dispersed), *Inga alba* (Leguminosae: mammal and bird-dispersed) *Stryphnodendron microstachyum* (Leguminosae: mammal-dispersed), *Simarouba amara* (Simaroubaceae: bird-dispersed), and *Vochysia ferruginea* (Vochysiaceae: wind-dispersed). In addition to stand manipulations for sustaining diameter growth, incorporation of regeneration requirements could keep at the same time, adequate levels of target species. Finally, forest modellers that are attempting to predict stand changes after logging should also benefit from research targeted at regeneration from seed to developing empirically-based probability functions for creating recruitment submodels (e.g., Pacala et al., 1996).

Perhaps now more than ever, natural forest management in the neotropics needs to be firmly rooted in biology. In many locations where timber is being exploited, ecological knowledge of tree regeneration is either still rudimentary or has not been properly transferred. Although applied research on tree seed ecology in logged forests is still much needed, implementation of what is known is likewise critical and may help to achieve a better balance between timber harvesting, biodiversity conservation, and the elusive goal of sustainable forest management.



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