

Anthropogenic disturbance in tropical forests: toward a functional understanding of seedling responses

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16.1 Introduction

The last decade has seen rapid growth in research dedicated to seedling ecology (Kitajima, 2007). This reflects an increased recognition of the importance of variation in seedling survival in determining patterns of adult abundance and distribution. Many seedling studies have grown out of larger programs investigating community dynamics in natural systems. Nonetheless, the results of these studies are often directly relevant to the management and conservation of human-altered ecosystems where changing environmental conditions and altered biotic interactions can directly affect seedling recruitment success. In extreme cases, human-mediated disturbances may be sufficient to invoke community-wide recruitment failure, leading to stalled succession or to shifts in vegetation type. Disturbance effects, however, can also have more subtle effects on recruitment success, resulting in changes in forest composition that may take decades or more to become apparent (Dirzo & Miranda, 1990).

Seedlings are particularly vulnerable to disturbance. Most species have no equivalent of the dormancy that facilitates seed survival through periods with adverse environmental conditions. Instead, alterations in light or soil moisture availability often impact seedlings first because their small leaf area and shallow rooting depth limit their ability to integrate resource capture over space. Similarly, only a small fraction of tree species have seed reserves that persist for more than a few months after germination, leaving seedlings vulnerable to damage and to temporal fluctuations in resource supply (Kitajima, 1996a; Harms & Dalling, 1997). Seedlings are also especially susceptible to natural enemies and fire. They may be less well defended or more accessible to herbivores than seeds and adults, and disease outbreaks may spread more rapidly through clustered populations.

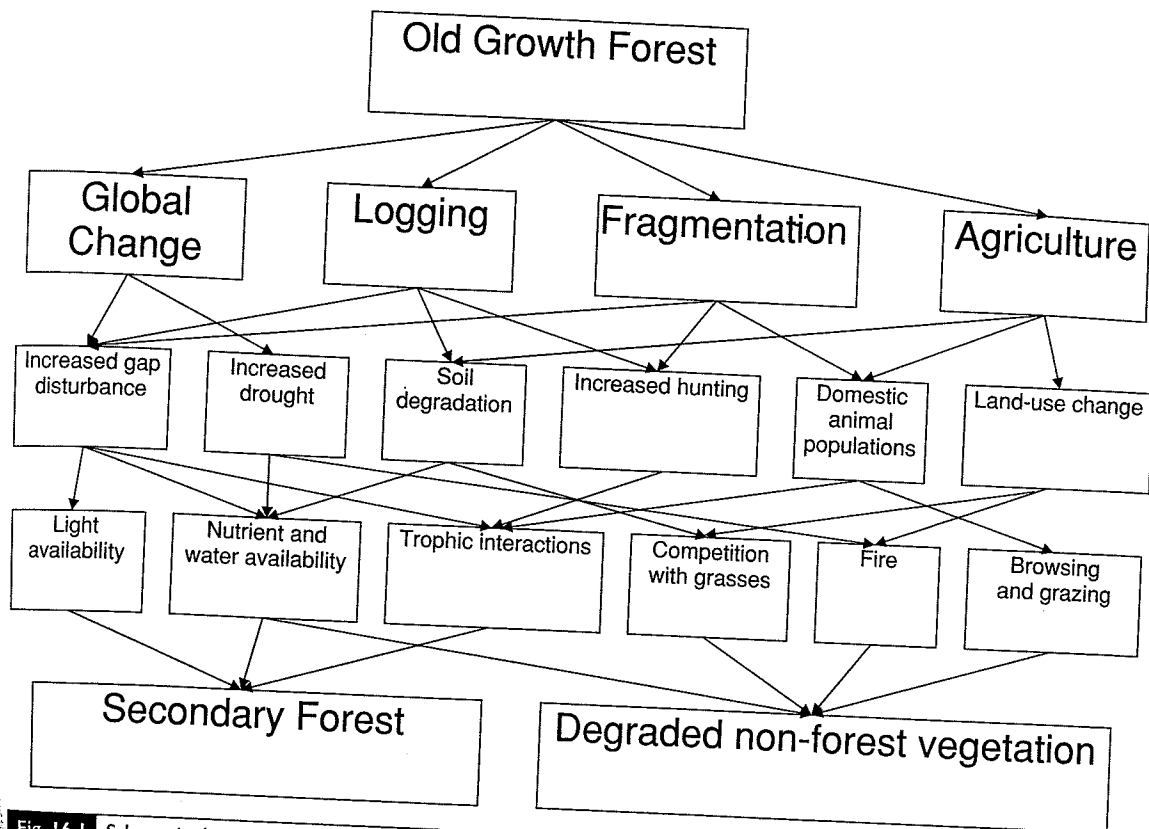


Fig. 16.1 Schematic diagram illustrating the pathways and mechanisms of forest responses to anthropogenic disturbance. We define four initial classes of disturbance that influence old growth tropical forests (level 1), their principal ecological effects (level 2), and mechanisms by which they influence seedling growth and survival (level 3). In turn, these effects collectively determine the variant of disturbed vegetation at a site (level 4). To improve clarity, we have illustrated only the most important linkages between levels, including all those discussed in the chapter. *Trophic interactions* include all biotic interactions (plant–herbivore, plant–pathogen, plant–mycorrhizal, plant–pollinator, and plant–dispenser) that contribute to the demography of seedlings in disturbed forests, except competition with grasses, ferns, and shrubs, which is considered separately. *Increased gap disturbance* includes both direct effects of gap creation on abiotic factors plus indirect effects of tree density on tree reproduction (see text for details).

seedlings than among more widely spaced adults (Gilbert *et al.*, 1999).

In this chapter, we highlight the different pathways by which human disturbances influence seedling recruitment (Fig. 16.1). Here we take a broad view of what constitutes anthropogenic disturbance: the direct effects of forest fragmentation, logging, and hunting have well-documented effects on seedling populations that can often be ascribed to individual processes. However, climate change is a disturbance affecting all forests. Increased tree growth and mortality rates in tropical forests reported over the last few decades should increase the frequency of canopy gap formation, a natural disturbance that influences the species composition of tropical forests. We also recognize that seedlings are not the only life stages affected by disturbance. Therefore, we start with a discussion of how disturbance impacts

populations. We then address the predominant mechanisms by which disturbance influences seedling recruitment patterns before examining in more detail the potential for species-specific responses. The focus of this chapter is on tropical forest ecosystems where seedling trait variation is high and the conservation implications of a functional understanding of seedling ecology is greatest. Understanding how disturbances associated with logging and with the cultivation and abandonment of agricultural lands affect seedlings will be of critical importance in the developing science of restoration ecology. Although our emphasis is on tropical forest ecosystems, recent work highlighting globally consistent variation among key plant functional traits (e.g. I. J. Wright *et al.*, 2004) implies that our comments should be generally applicable to other forests as well.

16.2 Significance of the seedling stage for forest management

In practice, the capacity of tropical forests to regenerate following disturbance may be more or less dependent on the seedling stage of the life cycle compared to other stages. In relatively undisturbed tropical forests, seed addition experiments have shown that, for most species, seedling recruitment is limited by the availability of seeds rather than suitable microsites for seedling regeneration (Makana & Thomas, 2004; Svenning & Wright, 2005). This result is also supported by seed trap studies that have shown that common tree species fail to disperse seeds to more than a small fraction of recruitment sites less than 100 m from reproductive adults (Hubbell *et al.*, 1999; Dalling *et al.*, 2002).

By disrupting the reproduction of forest trees, anthropogenic disturbance may exacerbate the relative importance of seed limitation, and thereby, change the relative importance of the seedling stage as a key factor for forest regeneration. Key disturbance effects on early life history stages are of three types, (1) reduced fecundity or seed dispersal, (2) reduced seedling growth or survival, or (3) reduced or expanded number and range of suitable microsites for germination and establishment. Type (1) impacts will exacerbate seed limitation at the population level, type (2) impacts are more or less neutral in terms of seed limitation but may shift the balance toward limitation by seedling survival, while type (3) impacts may increase microsite limitation for some habitat specialist species, while reducing microsite limitation for pioneer species and colonizers of disturbed soil and litter.

The main focus of this chapter is on seedling responses to disturbance and resource availability (types 2 and 3 impacts above), but seed or dispersal limitation may be exacerbated by anthropogenic disturbance and these impacts may represent the primary constraint on regeneration for some species. Logging results in direct loss of

reproductively mature trees of commercial timber species and accidental damage to noncommercial species. In addition, these individuals may become more isolated, thus reducing pollination success and outcrossing rates and increasing the frequency of inbreeding (Murawski *et al.*, 1994; Ghazoul, 2005). These impacts may collectively lower seed or fruit production. For example, seed production in logged forest was only 23% that of primary forest for dipterocarps in West Kalimantan, Indonesia (Curran & Webb, 2000), and was lower for individuals in logged compared to unlogged forests in Amazonia one decade after logging (Johns, 1992). Logging may also lower the densities of large vertebrate dispersers by reducing their food supply and/or destroying their habitat (Johns, 1997). This effect is particularly important in tropical forests where 65–90% of species are adapted for vertebrate dispersal (Willson *et al.*, 1989; Jordano, 1992). The increasing isolation imposed by forest fragmentation may also disrupt patterns of gene flow by pollination for facultative and obligatory out-crossing species and reduce genetic diversity of progeny by limiting the number of pollen donors (Dick *et al.*, 2003). Dispersal may also be reduced by fragmentation if the abundance or foraging patterns of animal dispersers are affected (Laurance, 2005). Consequently, seed production by plants may be lower in forest fragments (Aizen & Feinsinger, 1994).

Certain traits confer greater susceptibility to the negative effects of logging or forest fragmentation on seed production. For example, species that have relatively small and/or immobile pollinators (Ghazoul, 2005), have a dioecious breeding system (Mack, 1997), or exist at low population density (Ghazoul *et al.*, 1998) may show reduced pollination success in response to disturbance-induced reduction in the density of large adult trees. Similarly, trees with few, large fruits may be dispersed less effectively following disturbance because these species often depend on relatively few, large-bodied frugivores that are susceptible to hunting (Corlett, 1998; Laurance, 2005). Because most tropical trees exist at low population densities (<5 reproductive-sized individuals/ha), one or more of these traits is exhibited by a large proportion of tropical forest tree species (Turner, 2001). Therefore, although impacts of anthropogenic disturbance on seedling recruitment may contribute to population and community responses, effects on earlier stages in the life cycle may also be important.

16.3 Effects of human disturbances on seedling regeneration

Human disturbances can influence seedling growth and survival via numerous pathways. Direct effects include altered resource availability (light, moisture, and nutrients), physical damage to plants (fire, trampling), and compaction or removal of soil. Indirect effects

on plant communities are equally important and are mediated by changes in the range and frequency of biotic interactions between plants and their natural enemies (herbivores, seed predators, and pathogens) and between plants and their mutualists (pollinators, dispersers, and mycorrhizas).

Disturbance changes to canopy structure and light availability. Mature forests vary greatly in canopy structure and light availability. The amount and seasonal distribution of rainfall influence canopy deciduousness and herbaceous vegetation cover, while soil fertility and rates of natural disturbance (e.g. landslides, cyclones) additionally affect canopy stature and gap frequency (e.g. Hartshorn, 1980; Condit *et al.*, 2000; Stephenson & van Mantgem, 2005). The species composition of forests, to some extent, also reflects variation in structure and disturbance. Forests with low rates of canopy turnover lack fast growing pioneer species whose seedlings recruit exclusively in treefall gaps (Condit *et al.*, 1999). Conversely, when disturbances such as logging and forest fragmentation increase the frequency of gap formation, pioneer or longer lived shade-intolerant species proliferate (Laurance *et al.*, 2006). Molino and Sabatier (2001) showed how increased forest disturbance associated with logging in French Guiana can also influence species diversity. As the frequency of gap disturbance increased, so too did the proportion of recruits that were shade intolerant. However, because shade-intolerant species are a small fraction of species diversity, increasing opportunities for recruitment of these species beyond a threshold where both guilds coexist resulted in reduced stand species richness.

Increasing canopy disturbance may also affect stand species richness by promoting the establishment of lianas (woody vines). Most lianas are light demanding (Webb, 1958; Putz, 1984), and many recruit from seeds that await gap formation in the soil seed bank (e.g. Kennedy & Swaine, 1992; Dalling & Denslow, 1998). Increasing liana abundance potentially affects the recruitment of both shade-tolerant and shade-intolerant species, either by competing with trees for light and soil-borne resources (Stevens, 1987; Perez-Salicrup & Barker, 2000) or by smothering the surface of gaps, preventing seedling recruitment (Schnitzer *et al.*, 2000). Numerous studies have documented increased liana abundance in logged and fragmented forests in Queensland (Australia) (Laurance, 1991), Sabah, Malaysia (Campbell & Newbery, 1993), Atlantic coastal forest in Brazil (Viana *et al.*, 1997), and central Amazonia (Laurance *et al.*, 2001). However, liana abundance is also increasing in some forests with no recent human disturbance (e.g. over 10–20 years at 47 sites in western Amazonia, Phillips *et al.*, 2002; over 18 years in central Panama, S. J. Wright *et al.*, 2004; Wright & Calderón, 2006). These increases have been attributed to global climate change. Lianas may be more abundant because increasing atmospheric CO₂ concentrations have generally enhanced forest growth, resulting in higher stand turnover rates and greater recruitment opportunities for shade-intolerant species. Furthermore, lianas

may have an increased competitive growth response to elevated CO₂ (Condit *et al.*, 2006).

Changes in canopy structure affect seedling recruitment in the forest. Condit *et al.* (2000) summarized the spatial extent of seedling recruitment in lowland Amazonia, limited to a band of forest adjacent to the edge. Surveys conducted in the 1980s showed that woody tree species were little recruited and growth was slow, whereas seedling mortality was high. In contrast, shade-tolerant tree species were recruited lower at fragment edges than in the interior, and altered biotic interactions (e.g. increased seed predation) may have affected this (Benitez-Malvido, 1998).

Changes to soil structure and nutrient availability. Logging affects soil conditions. Logging disturbance affects 14–43% of liana forests in Malaysia, Indonesia, and Brazil, the most severely impacted areas. Logging for extraction, and the log transport, reduce soil nutrient availability. Logging also reduces soil nutrient rates, and increases soil erosion (Laurance, 1987; Malmer & Grip, 1999; Nussbaum *et al.*, 1995a).

The effects of soil disturbance on seedling recruitment varies depending on the extent of topsoil loss, and changes in soil structure and vegetation. Soil disturbance affects seedling recruitment when loss of topsoil eliminates the soil seed bank. Almost all tropical forest canopy gaps maintain seed banks for several months or some years (Dalling, 2005). Topsoil removal reduces soil porosity, reducing seedling recruitment. It has been reported for logged forests in Sabah (Malaysia). Skid trails reduce seedling recruitment of seeds in the seed bank. Seedling regeneration was lower in gaps created by logging equipment compared to natural gaps (Condit *et al.*, 2000). Conversely, logging may improve seedling recruitment by increasing surface litter, improving soil structure, or may improve seedling recruitment by damaging existing vegetation.

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may have an increased competitive advantage associated with a strong growth response to elevated CO₂ (Granados & Körner, 2002; Zotz *et al.*, 2006).

Changes in canopy structure may also affect conditions for seedling recruitment in the forest understory. Laurance *et al.* (2002) summarized the spatial extent of edge effects associated with fragmenting lowland Amazonian forest. Microclimatic effects were mostly limited to a band of forest less than 50 m from the forest edge and included reduced soil moisture and increased vapor pressure deficit. Surveys conducted in the same fragments showed that seedlings of woody tree species were little affected (Sizer & Tanner, 1999). Seedling recruitment and growth were elevated within 10 m of the edge, whereas seedling mortality was unaffected. However, overall, densities of shade-tolerant tree seedlings surveyed a few years later were lower at fragment edges than in the interior, perhaps resulting from altered biotic interactions (reduced seed output and dispersal and increased seed predation) rather than changes in resource availability (Benitez-Malvido, 1998).

Changes to soil structure and fertility

Logging affects soil conditions as well as light availability. Soil disturbance affects 14–43% of land surface area in conventionally logged forests in Malaysia, Indonesia, and Suriname (Pinard *et al.*, 2000). The most severely impacted areas are the skid trails created during log extraction, and the log landings, where logs are stored prior to transportation (Nussbaum *et al.*, 1995a). These disturbances typically result in reductions in soil nutrient availability, pore volume, and infiltration rates, and increases in soil bulk density and erosion rates (Lal, 1987; Malmer & Grip, 1990; Chauvel *et al.*, 1991; Douglas *et al.*, 1992; Nussbaum *et al.*, 1995a).

The effects of soil disturbance on the abundance and growth of seedlings varies depending on the degree of compaction, the extent of topsoil loss, and changes to soil surface characteristics and competing vegetation. Soil disturbance may inhibit post-logging forest recovery when loss of topsoil eliminates recruitment from seeds present in the soil. Almost all tropical pioneer species that dominate in large canopy gaps maintain seed banks that allow germination from seeds dispersed months or sometimes even decades prior to the disturbance (Dalling, 2005). Topsoil removal also affects residual soil fertility and porosity, reducing seedling growth and survival. Both effects have been reported for logged forest in the Ulu Segama Forest Reserve, Sabah (Malaysia). Skid trails that had lost their topsoil had lower densities of seeds in the seed bank (Howlett & Davidson, 2003) and seedling regeneration was lower in areas where topsoil had been removed by logging equipment compared to areas with intact topsoil (Pinard *et al.*, 2000). Conversely, soil disturbance may sometimes remove surface litter, improving establishment success from the soil seed bank or may improve seedling recruitment success if logging machinery damages existing vegetation (Fredericksen & Pariona, 2002).

Longer-term impacts of skid trails on forest regeneration have been studied in selectively logged forests in Costa Rica and Malaysia. In Costa Rica, there was a reduction in the density and diversity of stems ≥ 1 m tall and ≤ 5 cm dbh in the center of abandoned skid trails compared to plots on the edge of skid trails or in adjacent forest 12 to 17 years after logging (Guariguata & Dupuy, 1997). Similarly, skid trails in Sabah had lower richness and density of small woody stems (>1 m tall, <5 cm dbh) than adjacent unlogged forest 18 years after logging (Pinard *et al.*, 2000). In the Costa Rican study site, recovery of basal area on skid trails to values equivalent to the unlogged forest would take approximately 80 years. However, the responses of tree seedling establishment and growth to soil disturbance are still not well explored, and likely depend on interactions among logging practices, soil properties, and species traits.

Changes to fire regimes

Fires have always impacted tropical forests. However, the scale and frequency of tropical forest fires may be increasing because land use changes, such as logging (Holdsworth & Uhl, 1997; Curran *et al.*, 1999; Nepstad *et al.*, 1999; Siegert *et al.*, 2001) and habitat fragmentation (Cochrane & Laurance, 2002; Gascon *et al.*, 2000), increase susceptibility of forests to burn. Simultaneously, the number of ignition events is rising because of human colonization of formerly forested regions (Laurance, 1998) and because El Niño-related droughts are increasing in severity and frequency (Trenberth & Hoar, 1996; Dunbar, 2000). Surface fires in otherwise intact forest are difficult to detect remotely, but their effects are manifested in increased mortality rates of many components of the biota, including plants, invertebrates, and vertebrates (Laurance, 2003). Burning kills thin-barked (<1 cm thick) tropical forest plants directly, and seedlings are particularly at risk because of their small size (Uhl & Kauffman, 1990; Cochrane & Schulze, 1999). These direct effects may result in the death of one third of all trees greater than 10 cm dbh, and three quarters of all saplings, as well as many lianas and forbs during the first 15 months after fire (Barlow & Peres, 2004). Total tree mortality may increase to nearly 50% after 3 years, which leads to a collapse of forest biomass, increasing canopy openness and an invasion of light-demanding trees, shrubs, bamboos, and herbs at ground level (Barlow & Peres, 2004).

Recovery from fire may be inhibited by a positive feedback of fire on susceptibility to burning (Cochrane & Schulze, 1999). The increased canopy openness and greater quantity of necromass in once burned forests increases the likelihood that they will burn a second time and with greater intensity (Cochrane *et al.*, 1999; Slik & Eichhorn, 2003). In East Kalimantan (Indonesia), the density and diversity of understory trees were lower in forests that had burned twice (1982/1983 and 1997/1998) than in those that had only burned in 1997/1998 (Slik & Eichhorn, 2003). These changes lead to a cycle of degradation that ultimately eliminates forest cover and promotes the expansion of anthropogenic savanna, scrubland, and grassland (Laurance, 2003).

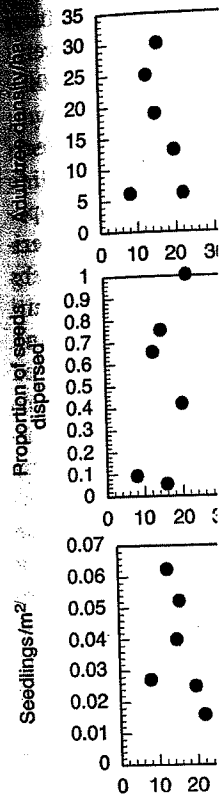


Fig. 16.2 Effects of *standleyanum* at sites i large rodent that cons Sites with low agouti consume seeds. (a) A seed dispersal was re recruitment increased poaching appears to f 5, and 6 in S. J. Wrig

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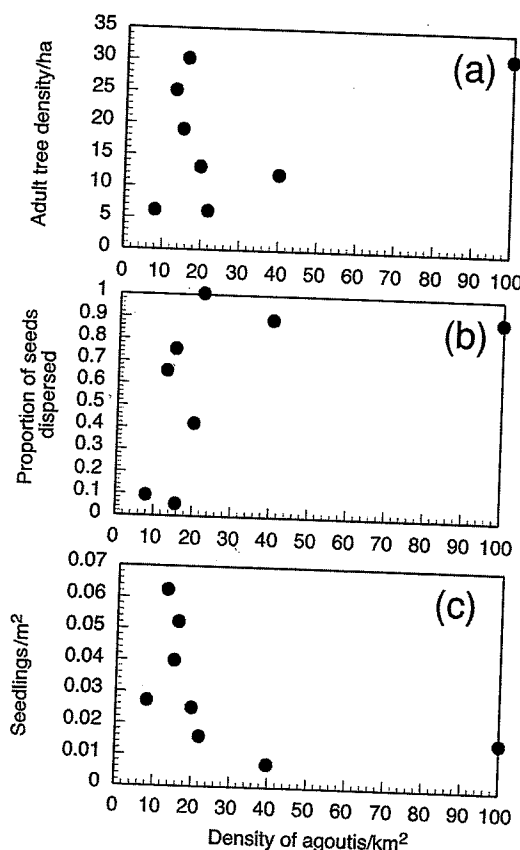


Fig. 16.2 Effects of poaching on recruitment of the canopy palm *Astrocarium standleyanum* at sites in central Panama. The density of agoutis (*Dasyprocta punctata*), a large rodent that consumes and disperses *Astrocarium* seeds, is plotted on the abscissa. Sites with low agouti densities also had low densities of other large mammals that consume seeds. (a) Adult *Astrocarium* density was unrelated to mammal density, but (b) seed dispersal was reduced at low mammal densities, and (c) *Astrocarium* seedling recruitment increased, reflecting reduced seed predation. Therefore, in the short-term, poaching appears to favor recruitment of this plant species. Redrawn from data in Figs. 2, 5, and 6 in S. J. Wright *et al.* (2000).

Changes to biotic interactions by hunting and forest fragmentation

Hunting can have dramatic effects on seedling communities by eliminating critical biotic interactions (Fig. 16.2; reviewed by Wright, 2003). Unrestricted hunting inside many protected areas in the tropics has removed entire guilds of herbivores, granivores, and frugivores (Robinson *et al.*, 1999; Peres, 2000, 2001; Dirzo, 2001). The effect of this defaunation on seedling communities was first studied in detail by Dirzo & Miranda (1990) in southern Mexico. They showed that a heavily defaunated site (Los Tuxtlas) had twice the seedling density but only a third of the understory species diversity of that found in a site

with an intact fauna (Montes Azules). Large effects of defaunation on seedling recruitment patterns have now been reported in several other tropical forests (Wright *et al.*, 2000; Roldán & Simonetti, 2001; Wright & Duber, 2001; Galetti *et al.*, 2006).

Forest fragmentation can have similar and often synergistic effects to hunting. Even large fragments (>1000 ha) may be too small to support populations of large carnivores resulting in elevated populations of herbivores and granivores (Terborgh, 1988). Several experiments have addressed how the trophic structure of tropical food webs influences plant recruitment. In Lake Gatun (Panama) and Lake Guri (Venezuela), islands of different sizes support subsets of the mainland fauna. In Lake Gatun, small islands (<1 ha) that have been isolated from the mainland for greater than 90 years support a highly impoverished tree community when compared to equal-sized patches of forest on the mainland (Leigh *et al.*, 1993). These islands support spiny rats (*Proechimys semispinosus*), but no larger resident mammals. Experimental studies to determine the causes of tree species loss on these islands have shown that seed predation rates and rates of seedling herbivory by mammals are higher on these islands than on the mainland (Asquith *et al.*, 1997; Asquith & Mejia-Chang, 2005). In Lake Guri, islands have been isolated for 20 years and allow a test of the early effects of a loss of large carnivores. Small islands at Guri (0.25–0.9 ha) lack carnivores but often retain large populations of a few generalist herbivores (e.g. tortoises, iguanas, and howler monkeys). On these islands, seedling and sapling densities are only a third of those found on large island and mainland sites. Low juvenile recruitment rates at Guri were attributed mainly to increased seedling herbivory by leaf-cutter ants, whereas seed predation rates appeared to be similar between island and mainland sites (Rao *et al.*, 2001; Terborgh *et al.*, 2006).

The variation observed in biotic responses to these disturbances argues for much more site-specific research to determine the causes of shifts in recruitment patterns. In forests where hunting and fragmentation primarily affect large frugivores, such as primates, fruit characteristics affecting diet choice in these animals may best predict effects on seedling recruitment via altered seed dispersal (Chapman & Onderdonk, 1998; Cordeiro & Howe, 2001). When terrestrial granivores and herbivores are most affected, as occurred in forests in Mexico and Panama, then the potential for small rodents less affected by fragmentation and hunting to compensate for the losses of larger mammals becomes important. For example, Wright *et al.* (2000) have suggested that the increase in seedling recruitment associated with hunting in Los Tuxtlas (Mexico), but not in Panamanian forests, may reflect the prevalence of spiny rats in Panama.

A striking contrast to tropical forests, where hunting has typically reduced densities of large herbivores (but see Ickes, 2001), occurs in boreal and temperate forests. In eastern North America, Europe, and Japan, deer populations have increased dramatically over the last century as a result of reduced hunting pressure, extirpation of natural

predators, and increased availability of winter forage from agricultural and silvicultural activities (Côté *et al.*, 2004). Deer browsing on seedlings and saplings can be sufficient to alter the chemical and physical defenses of plant populations (Vourc'h *et al.*, 2002), reduce species richness (e.g. Horsley *et al.*, 2003), and can lead to dramatic shifts in tree species composition (reviewed in Côté *et al.*, 2004). For example, seedlings and saplings of *Tsuga canadensis* (Pinaceae) are now rare across the upper midwestern USA, while virtually all seedlings greater than 30 cm tall of *Thuja occidentalis* (Cupressaceae) have disappeared (Rooney *et al.*, 2000, 2002). Remaining seedlings of these browse-sensitive species tend to be distributed on tip up mounds, rock faces, and other inaccessible microsites (Comisky *et al.*, 2005; Krueger & Peterson, 2006).

Changes to microbial communities

Disturbances that affect animal communities may also have cascading effects on pathogenic and mutualistic microbial communities. Browsing mammals and insects may be important vectors of plant diseases and can provide wounds that facilitate microbial infection (García-Guzmán & Dirzo, 2001; García-Guzmán & Benítez-Malvido, 2003). Changes to animal communities may also directly affect mycorrhizal communities. Mycorrhizas confer nutritional and other benefits to their hosts that are critical for seedling growth and survival and may potentially influence tree species community composition (Janos, 1980b; Kiers *et al.*, 2000; Chapter 9). In Australia and the neotropics, marsupials and rodents are important dispersers of spores of some mycorrhizas (Janos *et al.*, 1995; Reddell *et al.*, 1997; Mangan & Adler, 1999) and mammal exclosures in Australian rain forest show significant reductions in mycorrhizal diversity and density (Gehring *et al.*, 2002).

Logging damage to soils can also affect mycorrhizas. In a Malaysian forest, Alexander *et al.* (1992) found that logging reduced spore and inoculum density of arbuscular mycorrhizas and lowered the proportion of root length infected for bioassay plants. In Sabah, seedlings of the ectomycorrhizal species *Hopea nervosa* (Dipterocarpaceae) had the same proportion of infection but 40% greater morphospecies diversity when transplanted into unlogged (42) than logged (30) forest (Lee *et al.*, 1996; Alexander & Lee, 2005). Limited infectivity or functional diversity of mycorrhizas in forest soils may be an important potential constraint on forest recovery after logging.

16.4 Application of seedling functional ecology to tropical forest management and restoration

The expansion of agricultural land, urban development, and logging are leading to the loss of tropical forest at unprecedented rates

(Mayaux *et al.*, 2005; Kirby *et al.*, 2006). As a consequence, greater than 60% of tropical forests are now classified as secondary forest or degraded forest land (Chazdon, 2003). For ecologists, the imperative now is to learn how to manage the secondary forests that remain after logging and that develop after agricultural land has been abandoned. A shift in attention to tropical secondary forests will require an assessment of how ecological processes that determine seedling recruitment success might differ between primary and secondary forests, and further, how plant traits that confer a fitness advantage in mature forest environments might constrain recruitment success in degraded sites.

Research in mature tropical forests has identified three processes that potentially mediate seedling recruitment success: habitat specialization along gradients of resource availability (e.g. Kobe, 1999; Fine *et al.*, 2004), competitive interactions among plants (e.g. Lewis & Tanner, 2000), and frequency-dependent mortality arising from the activity of specialized natural enemies (e.g. Harms *et al.*, 2000). Here, we examine how seedling traits can influence the importance of these processes in determining regeneration success in disturbed forests.

Resource specialization: implications for forest management

A major unresolved question in forest ecology is whether habitat specialization can account for much of the local or landscape scale diversity seen in tree communities. Variation in resource availability (light, nutrients, and water) across habitat types might be expected to lead to selection on traits that maximize plant performance along portions of these resource gradients (Dalling & Burslem, 2005). The resulting performance trade-offs, where higher fitness under one set of conditions reduces fitness under another, may have a dominant effect on community structure (e.g. MacArthur & Levins, 1964; Tilman, 1988). Selection is expected to be strongest on seedling traits, as seedlings experience more variability in supply rates of light, water, and possibly nutrients than do adults or seeds. An understanding of performance trade-offs is of particular importance for forest management. If performance gradients are strong, then disturbed sites with altered resource supply rates may only allow the recruitment of a small subset of species in tree communities. Conversely, if performance gradients are shallow, then management practices may permit rapid recovery of species diversity and ecosystem function.

Seedling responses to light and moisture availability

Numerous studies reveal a performance trade-off between fast growth and low survivorship in high light, versus slow growth and high survivorship in shade (e.g. Hubbell & Foster, 1992; Kitajima, 1994; Kobe, 1999). Intensively logged or clear-cut forest should therefore stimulate the recruitment of the fastest growing pioneer species (e.g. *Trema* spp. Celtidaceae in the neotropics, Africa and Asia, and *Ochroma pyramidale* Malvaceae in the neotropics). These species require elevated or fluctuating soil temperatures for germination from seeds that can

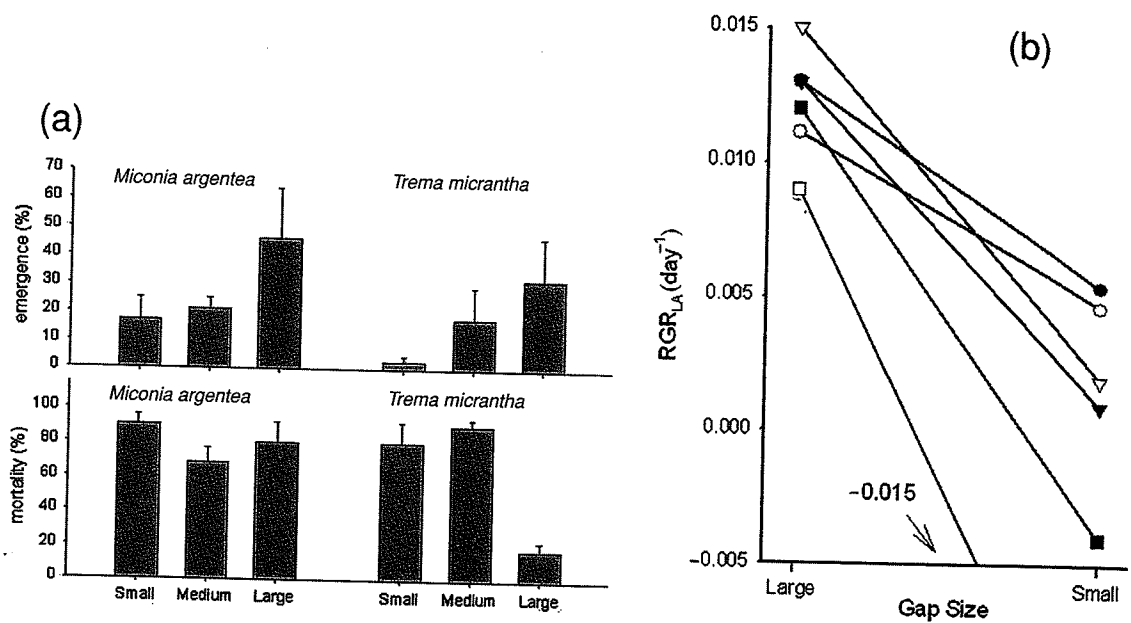


Fig. 16.3 (a) Mean and standard error emergence and seedling mortality after 10 weeks for seeds of *Miconia argentea* and *Trema micrantha* experimentally sown into small (25 m²), medium (64 m²), and large (225 m²) gaps on Buena Vista Peninsula (Panama). (b) Schematic illustration of the change in ranks of species relative growth rate of leaf area (RGR_{LA}) across gap sizes (small and large as above) for seedlings growing inside (closed symbols) or outside (open symbols) invertebrate herbivore enclosures over the first year following transplantation. ● – enclosed *Miconia argentea*, ○ – unenclosed *Miconia argentea*, ▼ – enclosed *Cecropia insignis*, □ – unenclosed *Cecropia insignis*, ■ – enclosed *Trema micrantha*, □ – unenclosed *Trema micrantha*. *Trema* showed poor germination, early seedling survival, and growth except in the largest gaps, while *Miconia* and *Cecropia* changed rank in growth rate between small (*Miconia*) and large (*Cecropia*) gaps. Redrawn from Pearson *et al.* (2003b).

persist in the soil for several decades after dispersal (Pearson *et al.*, 2002; Dalling, 2005; Fig. 16.3a). Smaller gaps, resulting from selective logging, and the partially shaded edges of forest fragments are often also colonized by pioneer species. Pioneers that occupy these sites are usually small seeded (e.g. *Cecropia* spp. Cecropiaceae, *Miconia* spp. Melastomataceae, *Piper* spp. Piperaceae) and detect canopy openings by discriminating small changes in red:far-red light ratio (e.g. Daws *et al.*, 2002). However, small seed size and light-sensitive germination prevents seedlings from successfully emerging from beneath leaf litter. Recruitment of these species may, therefore, also depend on disturbances that expose mineral soil (Vázquez Yanes *et al.*, 1990; Williams-Linera, 1990).

Changes in light availability may continue to affect species composition at the post-establishment phase and for decades after the initial disturbance. Fast growing species may become increasingly restricted to large gaps and clearings by either increased mortality or, in some cases, reduced growth in small gaps and forest edges, relative to competitors (Fig. 16.3b). Even once the canopy has regrown, spatial patterns of variation in light availability can differ from mature forests for several decades. For example, 20-year-old secondary forest in Costa

Rica had a larger fraction of microsites receiving intermediate light levels (2–5% full sun) than mature forest (Nicotra *et al.*, 1999). Changes in the availability of low to intermediate light microsites may strongly impact recruitment patterns of shade-tolerant species by increasing the availability of habitat where positive seedling growth rates can be maintained (Bloor & Grubb, 2003).

In contrast, recruitment of shade-tolerant species into high light microsites may be limited by the ability of seedlings to acclimate to high irradiance and leaf temperatures (Bazzaz & Carlson, 1982). Growth rates of seedlings of shade-tolerant species typically decline above 25–50% full sun (Veenendaal *et al.*, 1996; Poorter, 1999), partly due to photoinhibition, a temporary reduction in the efficiency of photosynthesis due to damage to photosystem II (Langenheim *et al.*, 1984). Species vary in susceptibility to photoinhibition in proportion to their shade tolerance (Krause *et al.*, 2001; Houter & Pons, 2005). However, longer-term experiments have shown that even strongly shade-tolerant species are able to survive exposure to full sun and acclimate to high irradiance conditions within a few months (Clearwater *et al.*, 1999; Krause *et al.*, 2006). Furthermore, after a prolonged period of acclimation, biomass growth of shade-tolerant seedlings may reach that of plants growing in partial shade (Krause *et al.*, 2006).

Photoinhibition, however, may contribute to recruitment failure when combined with water stress. In seasonal tropical forests, plants can experience considerable water stress during the dry season, indicated by low leaf water potentials (e.g. Chiarello *et al.*, 1987; Tobin *et al.*, 1999). These conditions may either be exacerbated in large gaps and clearings because of higher temperatures and vapor pressure deficits (Robichaux *et al.*, 1984), or ameliorated because of reduced root competition for water (Veenendaal *et al.*, 1995). In logged forests, soil compaction may also exacerbate seasonal water shortages by reducing soil pore volume or by affecting moisture release characteristics (Brooks & Spencer, 1997). These changes in soil moisture availability have the potential to exert large effects on plant communities. In a seasonally moist tropical forest in central Panama, experimental drought treatments have shown that seedlings of co-occurring species vary greatly in drought tolerance, with species from wet habitats especially susceptible to drought-induced mortality (Engelbrecht *et al.*, 2005). Even in aseasonal forests, dry spells of only a few days' duration may elevate seedling mortality in large gaps and clearings, with newly emerging seedlings with shallow rooting systems most susceptible (Engelbrecht *et al.*, 2006).

Seedling responses to nutrient availability

Tree species distributions are associated with soil factors at a variety of spatial scales (Clark *et al.*, 1999; Tuomisto *et al.*, 2003; Phillips *et al.*, 2003). In mature tropical forests, up to half the species in a local community may have distributions that are biased in relation to one or more soil nutrients (John *et al.*, 2007). Changes to soil structure and

fertility arising from compaction or erosion (Congdon & Harbohn, 1993; Nussbaum *et al.*, 1995a), or from atmospheric deposition of nitrate and sulfate (Driscoll *et al.*, 2003; Fabian *et al.*, 2005), might therefore strongly affect community composition. As yet, however, direct evidence of differential seedling responses to soil conditions in the context of these disturbances is rare. In the Ulu Segama Forest Reserve, Sabah, four tree species (two pioneer and two shade-tolerant dipterocarp species) were transplanted onto skid trails. The addition of either inorganic nutrients or forest topsoil increased the growth of all species (Nussbaum *et al.*, 1995b). This experiment supports the common finding that soil compaction may slow root growth and lower nutrient availability to plants (Greacen & Sands, 1980) and thus delay regeneration or reduce seedling growth (Malmer & Grip, 1990; Jusoff & Majid, 1992; Pinard *et al.*, 1996; Guariguata & Dupuy, 1997; Whitman *et al.*, 1997; van Rheenen *et al.*, 2004).

Predictions about the long-term effects of soil disturbances are also hampered by an inadequate understanding of the mechanisms underlying species differences in soil nutrient requirements. In short-term experiments, fast growing species from nutrient-rich habitats outgrow slow growing species from nutrient-poor habitats, even under oligotrophic conditions (Fichtner & Schulze, 1992; Keddy *et al.*, 1994; Baraloto *et al.*, 2006; dos Santos *et al.*, 2006). Over longer time scales, however, differences in whole-plant nutrient use efficiency might cause rank reversals of seedling growth under differential nutrient supply. Species specialization along soil fertility gradients may reflect a growth-mortality trade-off similar to that described for gradients of light availability. Fine *et al.* (2004, 2006) carried out experiments in which seedlings of species found in relatively nutrient-rich clay soil forests in Amazonia and congeneric species limited to nutrient-poor sand soils were transplanted into both habitat types. They found that the clay-soil specialists grew faster in both soil types, but were less resistant to herbivory, and suffered higher mortality than the better defended white-sand specialists (Fig. 16.4). This result may be exceptional because of the extreme variation in fertility between soil types. However, it has important implications for the restoration of forest cover on degraded soils. Matching species to restoration sites must be based on the soil conditions of their native habitats. In nutrient-poor environments, the selection of species with traits that confer defense against herbivores may be more important than selecting species for rapid growth rate.

On sites with the most highly degraded soils, growth rates of seedlings of pioneer species commonly used for restoration may be extremely low (Aide & Cavalier, 1994) and some amelioration of site conditions may be needed before forest cover can be restored. Fertilization of these sites with nitrogen or phosphorus may increase seedling growth rates (Gehring *et al.*, 1999; Davidson *et al.*, 2004). However, fertilization may also stimulate the growth of competing herbs and grasses with negative effects on woody seedling growth (Pareliussen *et al.*, 2006).

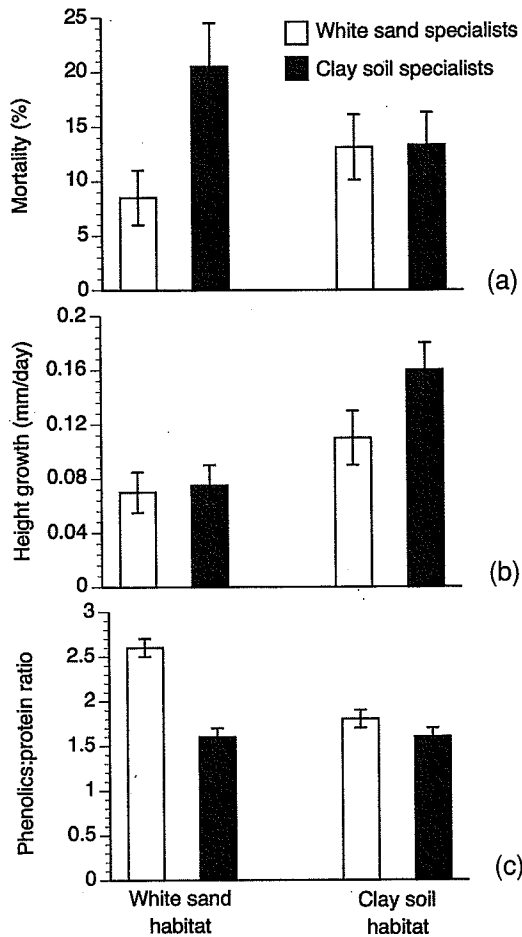


Fig. 16.4 Effects of soil type (fertile clay and infertile sand) on (a) percent mortality, (b) height growth, and (c) defense allocation for seedlings of 10 congeneric pairs of tree species, specialized to either sand or clay soils. Clay soil specialist species grew as fast as sand soil specialists on the nutrient-poor sand soils, but were less well defended from herbivores and suffered higher mortality rates. Redrawn from Fine *et al.* (2004, 2006).

Seedling responses to competition

In mature forests, competitive interactions among plants can strongly affect seedling growth. For example, in low fertility soils in central Amazonia, trenching around seedlings in the understory to remove root competition has a positive effect on seedling growth with a magnitude comparable to that of creating small canopy gaps (Lewis & Tanner, 2000). However, competitive effects on seedlings are mostly exerted by canopy vegetation, which intercepts most of the light and accounts for a large proportion of root biomass. There is little experimental evidence for competition for resources among understory seedlings (Wright, 2002).

In contrast, tree seedlings in pastures must often compete with grasses. Seedling transplant experiments show that lianas can have the strongest competitive effects (Slocum *et al.*, 2005). Similarly, establishment of *Charum*, *Pennisetum*, and *Melinis* reduces seedling recruitment (Aide *et al.*, 2000; Slocum *et al.*, 2000). In Panama, a combination of mowing and herbicide that *Saccharum spontaneum* reduces competitive effects on seedling growth. Small-seeded species were more successful in ground competition from *Saccharum*. More tolerant species performed well in these sites (Hooper *et al.*, 2002).

The selective barrier to tree species in abandoned pastures and natural gaps in Puerto Rico are dominated by *Urticaceae*, *Schefflera morototoni*, and *Melastomaceae* (Peterson *et al.*, 1995). Similarly, abandoned pastures are dominated by a species-poor community of *Clusiaceae*, while nearby secondary forests are dominated by a more species-rich community (Mesquita *et al.*, 2002).

The presence of competition is an important factor for stimulating tree growth in abandoned pastures. In lowland pastures, the stumps of trees that were cut for pasture patches (Peterson & Haines, 2002) also compete with tree seedlings. In the presence of fire and frequent fire, seedling establishment is reduced (Sri Lanka and *D. pectinatus*, 1995; Slocum *et al.*, 2006). In the presence of herbivores, they may catalyze seedling establishment by creating gaps (1991; Rhoades *et al.*, 1998) (Toh *et al.*, 1999; Slocum, 2000).

An alternative to stimulating tree growth is to circumvent grass cover. Grass cover slows seedling growth because of increased fire risk (2002; Lwanga, 2003), recruitment in active pastures in Africa. In active pastures in Africa, the use of large woody shoots

In contrast, tree seedlings in degraded forests and abandoned pastures must often compete with lianas, pasture grasses, or ferns. Seedling transplant experiments in logged forest in Ivory Coast show that lianas can dramatically reduce seedling growth, with the strongest competitive effects exerted belowground (Schnitzer *et al.*, 2005). Similarly, establishment of tall tropical grasses, such as *Saccharum*, *Pennisetum*, and *Melinis* (Poaceae) can often strongly inhibit seedling recruitment (Aide *et al.*, 1995; Holl *et al.*, 2000; Posada *et al.*, 2000; Slocum *et al.*, 2006). In abandoned pastures in central Panama, a combination of mowing and shading treatments showed that *Saccharum spontaneum* exerts both above- and belowground competitive effects on seedling recruitment (Hooper *et al.*, 2002). Small-seeded species were unable to tolerate either above- or belowground competition from *Saccharum*. In contrast, large-seeded, shade-tolerant species performed well and were recommended for reforesting these sites (Hooper *et al.*, 2002).

The selective barrier to recruitment imposed by grasses may in part explain the divergent successional trajectories observed between abandoned pastures and natural disturbances. For example, natural gaps in Puerto Rico are dominated by pioneer taxa (*Cecropia schrebiana* Urticaceae, *Schefflera morototoni* Araliaceae), whereas pastures become dominated by Melastomataceae, Rubiaceae, and Myrtaceae (Aide *et al.*, 1995). Similarly, abandoned pastures in Amazonia are colonized by a species-poor community dominated by the pioneer genus *Vismia* (Clusiaceae), while nearby secondary forests not used for pastures are dominated by a more species-rich community in which *Cecropia* is most abundant (Mesquita *et al.*, 2001).

The presence of competition-free microsites may be especially important for stimulating the recruitment of woody species in abandoned pastures. In lowland and montane forests in Costa Rica, small-seeded taxa (e.g. Melastomataceae) are restricted to nurse logs (often the stumps of trees that remained after pasture clearance) or fern patches (Peterson & Haines, 2000a; Slocum, 2000). However, ferns may also compete with tree seedlings on sites abandoned after human use and frequent fire, such as *Dicranopteris linearis* (Gleicheniaceae) in Sri Lanka and *D. pectinata* in the Dominican Republic (Cohen *et al.*, 1995; Slocum *et al.*, 2006). Once trees do become established in pastures, they may catalyze succession by modifying environments for seedling establishment both above- and belowground (Nepstad *et al.*, 1991; Rhoades *et al.*, 1998) and by providing perches for seed dispersers (Toh *et al.*, 1999; Slocum, 2001).

An alternative to stimulating regeneration on competition-free microsites is to circumvent the seedling stage altogether. When dense grass cover slows seedling recruitment or prevents establishment because of increased fire frequency (Cavalier *et al.*, 1998; Cabin *et al.*, 2002; Lwanga, 2003), recruitment can be started from large cuttings. In active pastures in Africa and the neotropics, farmers frequently use large woody shoots of resprouting tree species (e.g. *Gliricidia*

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sepium Leguminosae) as living fence posts planted directly into the soil (Budowski, 1987). Trials using these species indicate that many species can readily establish canopy cover and stimulate seedling recruitment in grass-dominated degraded pastures (Zahawi, 2005; Zahawi & Augspurger, 2006).

Seedling responses to natural enemies

Human disturbances frequently have large effects on populations of herbivores and granivores. However, impacts on seedling recruitment may be the hardest of all to predict. This is because compensatory effects often accompany the removal of suites of natural enemies and may have either positive or negative effects on focal plant species. For example, an important timber species and food source for mammal communities in Central American forests is *Dipteryx panamensis* (Leguminosae). In mature forests, *Dipteryx* seeds are dispersed by bats and primates, predated by mammals (squirrels and peccaries), and secondarily dispersed or predated by rodents (Bonaccorso *et al.*, 1980; Forget, 2004). Contrasting studies at nearby sites have shown either increased recruitment of *Dipteryx* in forest fragments, suggesting escape from mammalian seed predation (Hanson *et al.*, 2006), or increased seed predation and reduced recruitment (Guariguata *et al.*, 2002), suggesting ecological release of small granivorous rodents at sites where dispersers or large predator populations have been reduced by hunting.

The effects of altered herbivore and granivore communities are also likely to be influenced by seedling traits. Elevated seedling herbivory rates on small islands in Panama suggest that differences among species in tolerance or susceptibility to mammalian herbivory might contribute to the characteristic species composition of these sites (Leigh *et al.*, 1993; Asquith *et al.*, 1997). Similarly, differences in susceptibility to leaf-cutter ant defoliation might account for shifts in species composition on islands in Lake Guri (Rao *et al.*, 2001). Traits that confer resistance to foliar herbivory and browsing damage might include tough leaves, low nitrogen content, rapid leaf expansion, and early stem lignification (Coley, 1983; Kursar & Coley, 1991). Some of these traits may also confer resistance to fungal diseases (Augspurger, 1983; Benitez-Malvido *et al.*, 1999; Benitez-Malvido & Lemus-Albor, 2005), although these interactions remain poorly understood.

In mature forests, density-dependent mortality of seeds and seedlings appears to be an important constraint on adult population density (e.g. Augspurger, 1984b; Clark & Clark, 1984; Webb & Peart, 1999; Harms *et al.*, 2000). Not surprisingly therefore, attempts to improve the regeneration success of several important timber species in secondary forests have been hindered by pathogen and insect outbreaks to planted seedlings and saplings (e.g. *Swietenia* spp., *Khaya* spp. Meliaceae, *Stryphnodendron microstachyum* Leguminosae, *Melicia excelsa* Moraceae; Newton *et al.*, 1993; Folgarait *et al.*, 1995; Nichols *et al.*, 1998). However, the potential for compensatory density-dependent mortality arising from increased pathogen attack when herbivores and

granivores are absent has not been studied in tropical secondary forests. In both temperate and tropical forests, damping off pathogens can accumulate in the soil surrounding maternal sources of susceptible species (Augspurger, 1984b; Packer & Clay, 2000) and may develop populations rapidly in secondary forests (Packer & Clay, 2004). Therefore, when dispersers that remove seeds from the vicinity of maternal trees are absent, pathogen infection may further contribute to recruitment failure.

16.5 Future directions

Forest regeneration requires the successful completion of a sequence of steps between successive generations of reproductive adults. Consequently, the failure of tropical forests to regenerate following anthropogenic disturbance may be caused by disruption of any one or more of these steps, including floral induction, pollination, seed maturation, dispersal, germination, seedling establishment, growth or survival, and onward growth of saplings to reproductive maturity. The mechanisms that determine the transitions between these stages are not equally well understood, but land managers and conservation biologists need to recognize that barriers to forest regeneration may be occurring at any one or more of them. Research is required to understand the relative importance of these processes for a given site and to address potential solutions.

Our review has emphasized the sensitivity to anthropogenic disturbance of the processes that determine seed limitation and seedling recruitment, but this perspective is based on a limited number of case studies and is therefore necessarily anecdotal. In particular, because of the complexity of the biotic and abiotic interactions that impinge on tree reproduction, generalization beyond this level of detail may never be possible without detailed site-specific studies. The current state of knowledge suggests that seed limitation and seedling recruitment failure represent the most significant constraints on regeneration following anthropogenic disturbance; management of these problems is most likely to ameliorate the significant barriers to forest succession. However, further research is still required to address gaps in our understanding of how environmental conditions and biotic interactions affect the fate of individuals during seedling recruitment. The least well understood stages of plant life history are those that occur from primary dispersal to seedling emergence, which may include processes of secondary dispersal, seed burial, seed mortality due to pathogens, germination, and early seedling growth (e.g. Levey & Byrne, 1993; Gallery *et al.*, 2007; Marthews, 2007). Integrating this research with current knowledge of forest regeneration processes will require further development of mechanistic and spatially explicit forest simulation models typified by SORTIE and TROLL (Chave, 1999).

To circumvent seed limitation of forest regeneration and to manipulate species composition in favor of commercially valuable species,

land managers often resort to planting nursery-raised seedlings, despite the high costs of this approach (Lamb *et al.*, 2005). However, until recently the selection of species for reforestation or enrichment trials for degraded tropical lands has been biased toward well-known pioneers from a relatively small number of genera (Lamb *et al.*, 2005). The fundamental criterion for species selection has been the higher survival and growth of pioneer species in high light conditions (Poorter, 1999), which may reflect the greater susceptibility of shade-tolerant species to the short-term damaging effects of photoinhibition particularly when combined with water or nutrient shortage (Chiarello *et al.*, 1987; Tobin *et al.*, 1999; Bungard *et al.*, 2000). However, this emphasis on short-term biomass growth as the primary criterion for species selection in restoration programs may need to be reviewed. Recent research on the longer-term responses of tree seedlings to photoinhibition has highlighted how relatively shade-tolerant species can reach maximal rates of biomass accumulation in open conditions (Clearwater *et al.*, 1999; Krause *et al.*, 2006).

More generally, optimizing survival in sites with low nutrient or water availability may require experimentation with species that use these resources conservatively (Craven *et al.*, 2007) and possess an allocation strategy that emphasizes defense against natural enemies and capture of belowground resources over fast growth rates. These traits are more often found in relatively shade-tolerant species, which may, therefore, have greater potential for restoration of degraded tropical lands than previously supposed. A comparison of the growth and survival of seedlings of 18 tree species planted into clearings in fern thickets on infertile post-agricultural soils in Dominica found that the species with the highest survival over 3 years, *Inga fagifolia* (Leguminosae), a late-successional nitrogen-fixer, and *Alchornea latifolia* (Euphorbiaceae), were ranked third and sixth in terms of growth rate over the same interval (Slocum *et al.*, 2006). In the most degraded or exposed sites, such species may require amelioration of site conditions by an established canopy of a species that can tolerate high light combined with low water and nutrient availability. For example, in the lowland wet zone of Sri Lanka, a wide range of relatively shade-tolerant herbaceous and tree species establish successfully as seedling transplants beneath a canopy of thinned *Pinus caribaea* (Pinaceae) plantations on degraded sites previously dominated by pasture grasses (Ashton *et al.*, 1997, 1998). Although we do not advocate the widespread planting of exotic species such as *Pinus caribaea* in Sri Lanka, trials with native species with similar traits may prove fruitful as part of a two-stage process for restoring the most degraded sites.

Our perspective on forest restoration has two fundamental implications for the direction of future research. First, the response of tree seedlings to anthropogenic disturbance may be unpredictable on the basis of current knowledge because different types of disturbance vary in their effects on the biotic and abiotic environment and are highly site specific. Although seedling growth in response to abiotic resource supply should be predictable, survival is less easily predicted when

anting nursery-raised seedlings, each (Lamb *et al.*, 2005). However, species for reforestation or enrichment has been biased toward well-known number of genera (Lamb *et al.*, 2005). Pioneer species in high light conditions reflect the greater susceptibility of tree seedlings to damaging effects of photoinhibition with water or nutrient shortage (Bungard *et al.*, 2000). However, growth as the primary criterion for species selection may need to be reviewed. Responses of tree seedlings to shade, particularly shade-tolerant species, may vary with accumulation in open conditions (Lamb *et al.*, 2006).

Tree seedlings in sites with low nutrient availability and low light availability, particularly those that use shade-tolerant species (Lamb *et al.*, 2007) and possess an allopathic response against natural enemies and fast growth rates. These traits are characteristic of shade-tolerant species, which may be important for the restoration of degraded tropical forests. A comparison of the growth and survival of tree seedlings planted into clearings in forest soils in Dominica found that, over 3 years, *Inga fagifolia* (Leguminosae) and *Alchornea latifolia* (Euphorbiaceae) ranked sixth in terms of growth rate (Lamb *et al.*, 2006). In the most degraded sites, tree seedlings require amelioration of site conditions. Tree seedlings that can tolerate high nutrient availability. For example, in Dominica, a wide range of relatively shade-tolerant species establish successfully in clearings of thinned *Pinus caribaea* stands previously dominated by pasture. Although we do not advocate the use of tree species such as *Pinus caribaea* in similar sites, similar traits may prove fruitful for the restoration of the most degraded sites. This research has two fundamental implications. First, the response of tree seedlings to shade may be unpredictable on the different types of disturbance vary with site conditions and are highly variable in response to abiotic resource availability. Second, it is less easily predicted when

it is determined by the abundance of natural enemies rather than abiotic resources. Second, if natural enemies are important determinants of seedling responses to anthropogenic disturbance, then a diverse seedling community from an early stage may serve as an insurance against the unpredictability in response to interactions at higher trophic levels (Montagnini *et al.*, 1995). Seedling community diversity may also be desirable if it promotes early reestablishment of ecosystem function (Erskine *et al.*, 2006) and gives rise to mixed forests that facilitate regeneration of a diverse plant community (Carnevale & Montagnini, 2002). However, these topics remain poorly explored aspects of tropical forest restoration ecology.

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