ELSEVIER

Forest Ecology and Management 148 (2001) 185–206

Forest Ecology and Management

www.elsevier.com/locate/foreco

Neotropical secondary forest succession: changes in structural and functional characteristics

Manuel R. Guariguata[a,*], Rebecca Ostertag[b,c]

[a]Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Unidad de Manejo de Bosques Naturales, 7170 Turrialba, Costa Rica
[b]Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720-3110, USA
[c]International Institute of Tropical Forestry, USDA Forest Service, Rio Piedras, PR 00928, USA

Received 27 March 2000; accepted 7 June 2000

Abstract

In this review, we highlight the main biotic and abiotic factors that influence the patterns of Neotropical secondary forest successions, referred as the woody vegetation that regrows after complete forest clearance due to human activities. We focus on both patterns of species replacement and various processes that occur during succession, and suggest that the sequence of processes may be predictable even if species composition is not. We describe forest recovery with respect to old-growth conditions, which we define as the structure, function, and composition of the original forest before conversion, and we examine this recovery process within the context of type and intensity of past land use. The various phases of the recovery process are described in detail: from factors affecting early colonization, changes in light and soil properties, soil–vegetation feedbacks at initial and later successional stages, biomass accumulation, forest productivity, rates of species accumulation, and species composition. The consensus of these analyses is that the regenerative power of Neotropical forest vegetation is high, if propagule sources are close by and land use intensity before abandonment has not been severe. Nevertheless, the recovery of biophysical properties and vegetation is heavily dependent on the interactions between site-specific factors and land use, which makes it extremely difficult to predict successional trajectories in anthropogenic settings. We attempt, throughout this review, to integrate the structural and functional characteristics of secondary succession as a way to enhance our ability both to predict and manage successional forest ecosystems due to their increasing importance as timber sources, providers of environmental services, and templates for restoration purposes. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Biomass; Forest productivity; Forest regeneration; Forest succession; Land use history; Land use intensity; Neotropics; Pasture conversion; Tropical soils; Tropical rainforest

1. Introduction

Tropical secondary forests are important as timber sources (Finegan, 1992; Hutchinson, 1993; Wadsworth, 1997), providers of environmental services such as protection from erosion and atmospheric carbon fixation (Fearnside and Guimaraes, 1996), templates for forest rehabilitation (Lugo, 1992), refugia of plant biodiversity in fragmented landscapes (Lamb et al., 1997), and as local providers of medicinal and useful plants (Toledo et al., 1995; Voeks, 1996; Chazdon and Coe, 1999). In addition, the area of tropical secondary forest is predicted to increase in the next century due to industrialization and urbanization

---

[*] Corresponding author. Tel.: +506-556-0401;
fax: +506-556-2430.
E-mail address: mguarigu@catie.ac.cr (M.R. Guariguata).

PII: S0378-1127(00)00535-1

processes, which often lead to an abandonment of agricultural activities (e.g., Thomlinson et al., 1996). Because of fast-growing properties of secondary forests and the current pressures on old-growth forests in many Neotropical locations, they hold enormous but yet untapped management potential. Although we recognize that legal aspects (e.g., Müller, 1998) as well as technical and political interventions (e.g., Smith et al., 1998) play a key role in influencing secondary forest utilization in the Neotropics, there is still a tremendous need to understand and further refine our knowledge of ecological processes involved in secondary succession, so that such processes can be adequately considered in the management of this resource.

Secondary forest succession has been extensively described throughout the lowland Neotropics for many decades (e.g., Kenoyer, 1929; Standley, 1937; Budowski, 1961) and understanding how forests recover after clearance is still a current research topic both for basic and applied purposes (e.g., Nepstad et al., 1990; Brown and Lugo, 1990a; Lugo, 1992; Finegan, 1996; Holl, 1999). Most commonly, the structural characteristics of the developing forest (e.g., basal area, biomass, species richness, and species composition) are studied, and occasionally functional characteristics (e.g., nutrient cycling, net primary productivity, understory light environments) are measured. This bias has allowed secondary forests to be relatively well defined from a structural perspective, relative to old growth conditions (Corlett, 1994; Clark, 1996; see Table 1). Despite the theoretical framework, there has been little scientific integration of the structural and functional characteristics and processes that occur during secondary succession. Much of the emphasis in secondary succession has focused on which species or group of species dominate which stages of succession (see, e.g., descriptive models by Gómez-Pompa and Vázquez-Yanes, 1976; Finegan, 1992). From a functional perspective, however, ecosystems may recover functions long before they recover, if any, floristic similarity to previous conditions. For example, growth of roots, regardless of species, may serve to reduce soil erosion and allow plants to uptake nutrients that might otherwise be leached. In addition, recovery of leaf area through the growth of the forest canopy casts shade, reducing soil temperature and soil water evaporation. This functional perspective to examining succession stems from the hypothesis that there is ecological redundancy among plant species, i.e., from an ecosystem standpoint many plant species can perform similar functions (Walker, 1992). Thus another way to approach secondary forest succession is to ask when ecosystem function returns to pre-disturbance levels. The objective of this review is to mesh and discuss both changes in structure and function, and to highlight questions requiring further research.

2. Definitions

We refer to secondary forest succession as the woody vegetation that regrows after complete forest clearance for pasture, agriculture, or other human activities such as clearcutting for pulp (Faber-Langendoen, 1992) or timber (Gorchov et al., 1993). We are aware that the human factor adds considerable

Table 1
Structural characteristics of lowland tropical rainforest as a function of age since disturbance (adapted from Clark, 1996)

Characteristic	Young secondary forest	Old secondary forest	Old-growth forest
Stand basal area	Lowest	Intermediate	Highest
Distribution of tree stem diameters	Lowest coefficient of variation (CV)	Intermediate CV	Highest CV
Canopy structure	Even canopy, few gaps	Even canopy, small gaps common	Variable canopy height, gaps more frequent
Lianas/epiphytes	Absent	Rare	Common
Large logs	Present or absent	Usually absent	Always present
Very large trees	Usually absent except as obvious remnants	Usually absent	Always present

complexity to the process of forest succession, and we will emphasize the effects of type and intensity of past land use throughout this paper. Our focus is also heavily slanted towards the moist and wet lowland forests, because most research in the Neotropics has been conducted on this region. There is no reason to expect, however, that the patterns described here also apply to drier zones. For recent studies on secondary dry forest succession see, e.g., Rico-Gray and Garcia-Franco (1992) and Mizrahi et al. (1997).

In general terms, secondary forest succession is influenced by stochasticity, a species' biology, and its interaction with other species (either between plants, or between plant and animals), and by the interplay of biotic and abiotic components (vegetation and climate). All these factors ultimately determine a particular floristic composition at a given age (stage) and also influence the degree of structural and functional recovery of the original vegetation. Therefore, secondary forest succession can be visualized as a continuum from an early stage where the factors that govern colonization are most important (i.e., substrate conditions for germination, timing of seed arrival via off-site dispersal, presence of soil-stored seeds and resprouts), to later stages where competitive ability and tolerance of environmental conditions among species (determined primarily by species-specific growth rates, longevity, maximum size at maturity, and degree of shade tolerance) largely dictate patterns of species replacement over time (Walker and Chapin, 1987).

By using the term "recovery", we do not mean to imply that these forests will return to identical pre-abandonment conditions, but rather that they will recover to a functioning forest ecosystem that may or may not contain the original species composition. This old-growth forest will not be a static ecosystem, but will be subjected to a variety of chronic disturbances that alter structure and function such as canopy gaps (Denslow, 1987), landslides (Garwood et al., 1979), hurricanes (Brokaw and Grear, 1991), and river meanders (Salo et al., 1986). In addition, we recognize that many Neotropical areas that currently support old-growth forest are not free of the effects of past disturbance (Denevan, 1992) and are in fact, the product of centuries-old secondary succession following the abandonment of agricultural fields (e.g., Bush and Colinvaux, 1994).

3. Major patterns of floristic and structural recovery

Much of our understanding of the vegetation dynamics during Neotropical secondary forest succession has been influenced from pioneering studies on small-scale, slash-and-burn agriculture, particularly in lowland Central America (Budowski, 1961; Snedaker, 1970; Ewel, 1971, 1976; Tergas and Popenoe, 1971) and in Amazonian *terra firme* forest (Uhl et al., 1982; Uhl and Clark, 1983; Uhl, 1987). It is important to keep in mind that although the patterns described below are fairly general, slash-and-burn succession is strongly influenced by the combination of proximate seed sources (both off- and on-site), and relatively low intensity of use of previous abandonment. In extensive (fire-prone) abandoned cattle pastures, or in severely degraded areas, successional trajectories are likely to differ, and the recovery of ecosystem structure and function is expected to be much slower (e.g., Uhl et al., 1988). We will repeatedly discuss the effect of land use type and intensity on ecosystem structure and function throughout the rest of this paper.

The first decade of forest succession after site abandonment in the lowland moist and wet Neotropics is characterized by vegetation dominated by grasses, shrubs, and forbs, which are eventually shaded out by short-lived, light-demanding "pioneer" tree species, in particular *Cecropia*, *Ochroma*, and *Solanum* and many tree species in the Melastomataceae and Rubiaceae. After this period, the canopy is dominated by long-lived, taller-statured, but nevertheless light-demanding tree species in the genera *Alchornea*, *Cordia*, *Goupia*, *Inga*, *Jacaranda*, *Laetia*, *Simarouba*, *Spondias*, *Trema*, *Vochysia*, and *Vismia*, and sometimes much larger-sized and even longer-lived species such as *Cavanillesia*, *Ceiba*, and *Ficus* (Lang and Knight, 1983; Finegan, 1996). Because most of these tree species are unable to grow and/or reproduce under their own shade (Knight, 1975; Saldarriaga et al., 1988), their canopy dominance is constrained to early colonization after site abandonment. Eventually, the canopies of these secondary stands may be replaced by other shade tolerant species characteristic of old-growth forest that usually germinate and establish during early succession (Knight, 1975; Guariguata et al., 1997; Denslow and Guzman, 2000). Yet, it may take centuries for secondary succession to resemble the floristic composition of old-growth forest (but not in terms of species richness as described below). For example, in an 80-year forest succession chronosequence after slash-and-burn in the Venezuelan Amazon, Saldarriaga et al. (1988) observed that saplings of tree species characteristic of old-growth forest started to dominate in abundance not before 60 years post-abandonment.

Almost uniformly, young stands are characterized by higher tree densities, lower basal areas, and shorter canopy heights (Saldarriaga et al., 1988; Aide et al., 1996; Denslow and Guzman, 2000) compared to old-growth forest. However, variation in tree basal area and biomass may follow either an asymptotic increase with respect to old-growth forest (Saldarriaga et al., 1988; Aide et al., 1996; Hughes et al., 1999), or peak at intermediate aged stands (Denslow and Guzman, 2000). We discuss below the details and mechanisms behind all these successional patterns so far described (most of them are presented in summary fashion in Table 2).

4. Initial colonization stages

4.1. Sources of plant regeneration: the seed bank

Buried seeds in the soil, as well as recently dispersed seeds, contribute to the development of secondary vegetation. However, the share of soil-stored seeds to forest regrowth appears more important (see review in Garwood, 1989), especially when land use intensity before abandonment has been low-to-moderate. Even though the density of soil-stored seeds is reduced when the site has been burned (Ewel et al., 1981; Uhl et al., 1981), its contribution to immediate post-disturbance regrowth is usually much more than that of recently dispersed seeds for most species (Young et al., 1987). Increased levels of incident light (accompanied by shifts in light spectral quality) and/or temperature stimulate seed germination (Raich and Gong, 1990; Vázquez-Yanes and Orozco-Segovia, 1994) of early colonizing species (but see Guariguata, 2000). Although there is large variation in seed longevity in the soil in those tree species that dominate secondary stands, it usually does not exceed 1 year after dispersal (Alvarez-Buylla and Martinez-Ramos, 1990; Dalling et al., 1997, 1998; Guariguata, 2000). Thus, canopy dominance of light-demanding tree species during secondary succession is largely dependent on recent seed dispersal following site abandonment. Therefore, the probability of site colonization may be low for those tree species that either do not reproduce annually, or that are located at a critical distance, as spatial limitations to seed dispersal into open areas may be very strong only a few meters beyond the forest–non-forest interface (e.g., da Silva et al., 1996). Phenological differences in seed availability and seed longevity in the soil, and dispersal limitation, may account for the large dissimilarities in canopy composition in secondary stands of both comparable age and previous land use history (Saldarriaga et al., 1988; Guariguata et al., 1997).

As intensity of land use increases, the potential of secondary forests to regenerate from soil-stored seeds concurrently diminishes. For example, Aide and Cavelier (1994) suggest that in severely degraded grasslands in the Sierra Nevada de Santa Marta, Colombia, forest regeneration from the seed bank is of minimal importance (attributed to chronic burning). Intensity of land use also influences the floristic composition of the seed bank that may originate a given plant community after site abandonment. Usually, the vegetation that develops right after clearing of old-growth forest (i.e., minimal land use intensity) tends to be poorer both in terms of species richness and abundance than that arising from cleared sites previously supporting successional vegetation (Young et al., 1987; Quintana-Asencio et al., 1996). The dominant type of land use in the surroundings may also influence both qualitatively and quantitatively seed bank populations at a particular location. For example, the floristic composition and density of soil-stored seeds in secondary forests close to agricultural or otherwise deforested land is known to contain large amounts of light-demanding shrub and herbaceous species (e.g., Cheke et al., 1979; Dupuy and Chazdon, 1998). In contrast, the soil seed bank of secondary forests that have been historically surrounded by old-growth forest may show a smaller proportion of herbaceous, “weedy” taxa (Dalling and Denslow, 1998). The high abundance of non-tree taxa in the soil seed bank may have important implications for timber management of secondary forests (e.g., Guariguata, 2000). Because most of their component canopy species are unable to regenerate in the

Table 2
Proposed relative importance of selected regeneration mechanisms/processes and structural/functional attributes as a function of past land use intensity during Neotropical secondary forest succession

Intensity of past land use	Regeneration mechanisms/processes				Structural/functional attributes		
	Seed bank	Remnant trees	Stump resprouts	Seed predation[a]	Recovery of species richness	Rate of biomass accumulation	Recovery of soil nutrients
Low (small, slash-and-burn patches)	High[b,c]	Low[d]	High[c,e]	High[f]	Rapid[g,h,i]	Rapid[j,k]	Rapid[k,l]
High (extensive pastures)	Low[m,n,o,p]	High[q]	Medium/Low[o]	High[r,o]/Low[n]/Unimportant[s]	Slow[l]	Slow[i,k]	Slow[k,l]

[a] With respect to adjacent forest.

[b] Ewel et al. (1981), Young et al. (1987).

[c] Uhl et al. (1981).

[d] Due to relative proximity to forest seed sources.

[e] Uhl and Jordan (1984), Kammesheidt (1998).

[f] Uhl (1987).

[g] Particularly for small-sized plant classes, not necessarily for larger individuals.

[h] Guariguata et al. (1997), Saldarriaga et al. (1988).

[i] Uhl et al. (1988).

[j] Fearnside and Guimaraes (1996).

[k] Silver et al. (2000), Buschbacher et al. (1988).

[l] Hughes et al. (1999), Weaver et al. (1987).

[m] Not necessarily in terms of quantity, but quality (prevalence of tree seeds from adjacent forest).

[n] Aide and Cavelier (1994).

[o] Nepstad et al. (1996).

[p] Due to their role as providers of perching sites for avian dispersers, as seed dispersal rates declines drastically from forest to pasture.

[q] Vieira et al. (1994), Guevara et al. (1992), Harvey (2000).

[r] These discrepancies are probably due to differences in both the extent of site degradation, and degree and type of plant cover.

[s] Holl and Lulow (1997).

understory, drastic canopy removal seems necessary for sustained tree regeneration after timber harvesting; but at the same time, there is a high potential for competing vegetation that arises from the seed bank to interfere with tree seedling establishment and growth once the canopy has been opened. This scenario is likely to occur in secondary stands as a rule, as they are usually located within agricultural land.

4.2. *Effects of remnant vegetation*

The presence of remnant vegetation can strongly influence the rate of initial colonization through its effects on seed dispersal. In extensively deforested areas such as cattle pastures, spatial constraints to seed dispersal emerge as one of the critical barriers to succession. In Colombia, Aide and Cavelier (1994) quantified virtually no dispersed seeds in pastures at only 20 m away from the nearest forested patch. Similarly, Holl (1999) concluded that dispersal limitation — and not impaired seed germination due to inadequate substrate conditions — was the critical factor limiting plant colonization in a Costa Rican abandoned pasture. Thus, it is not surprising that isolated remnant trees and fruit-bearing shrubs play an important role in site colonization by serving both as perches and food resources for seed dispersers, especially birds (Terborgh and Weske, 1969; da Silva et al., 1996; Harvey, 2000). In Mexico, Guevara et al. (1992), and Guevara and Laborde (1993) found that plant species whose fruits are dispersed by birds and bats were over-represented underneath remnant trees in pastures, which, at the same time, may facilitate their germination and establishment due to favorable microclimatic conditions under their canopies. Similarly, in Amazonian pastures, Vieira et al. (1994) report that underneath *Cordia multispicata* shrubs, a common colonizer, soil fertility and rates of seed deposition by avian dispersers would favor succession at much faster rates than in adjacent locations dominated by grasses. An application of this research has been to provide artificial perching structures in order to accelerate seed deposition in pastures (Aide and Cavelier, 1994; Holl, 1998).

When site conditions are highly degraded or seed sources are distant, plantation establishment may be a better way to ensure forest cover than natural succession. Furthermore, plantations can have many of the same functions as secondary forest or even exceed secondary forest in terms of plant productivity (Lugo, 1992, 1997; Fu et al., 1996). The establishment of tree plantations has been suggested as a means to accelerate succession of forest understory communities through the elimination of weed competition while attracting seed dispersers (Parrotta, 1992; George et al., 1993; Kuusipalo et al., 1995; Fimbel and Fimbel, 1996; Keenan et al., 1997). However, the use of plantations to recover properties such as soil fertility, forest structure, and understory species richness will depend on economics and on management objectives. For example, Murcia (1997) observed in the Colombian Andes that the understory of patches of the nitrogen fixing species, *Alnus acuminata*, were less species rich (presumably due to high N levels in the soil) than adjacent sites of similar age that underwent natural succession. Planting *Alnus* can nonetheless be beneficial due to its role in enhancing soil N levels in highly eroded sites if recovery of species richness is not an immediate goal. In contrast, in plantations in Hawaii, many non-native plant species invaded the understory (Harrington and Ewel, 1997), which in that case belied management objectives. What we do know from these efforts is that the species composition of the plantation overstory affects the quantity and quality of understory woody regeneration (e.g., Guariguata et al., 1995; Powers et al., 1997; Parrotta and Knowles, 1999), and thus with an understanding of the species' characteristics it may be possible to choose plantation species that will lead to rehabilitation of both species richness and site quality.

In contrast to seeds, the contribution of resprouted stems to stand structure and floristics during secondary succession has been little studied. Resprouts are likely to be important in forest regeneration as many species are capable of producing either sprouts originating from boles or branches (aboveground sprouts) or subterranean tissues (root sprouts). In sites in Paraguay and Venezuela, Kammesheidt (1999) showed that "secondary" and "primary" forest species, as well as trees occupying the understory, mid-canopy, and canopy are all capable of resprouting. Because so many species were able to resprout, there was no significant relationship between a species' successional status and resprouting ability (Kammesheidt, 1998). Of the species that do resprout though, "secondary forest" species seemed to show a higher proportion of resprouting than primary forest species (Kammesheidt, 1998).

Empirical studies of the abundance of resprouted stems versus stems that establish from seed are scant in successional forests. Previous works have reported that the abundance of resprouted stems is similar or sometimes greater than stems that originated from seed in young stands (Uhl et al., 1981; Uhl and Jordan, 1984). Yet, the fate of these resprouts over time is not clear due to the paucity of longer-term data. Saldarriaga et al. (1988) observed in slash-and-burn succession that resprouts were more easily detected (but not necessarily more abundant) in younger stands. As succession proceeds, however, the abundance of species that colonize via seeds is expected to overwhelm the abundance of resprouts if no further cutting is involved. The paucity of sprouts in old stands may also be due both to delayed mortality either due to past fire effects or pathogen invasion through the stump. In moist forest in Paraguay, resprouting stems in 2–5-year-old fallows were about twice as common as seed-established individuals, but in 10- and 15-year-old fallows, an approximately equal proportion of stems was from seeds and sprouts (Kammesheidt, 1999).

4.3. Post-dispersal seed fate

After seeds are dispersed, another important obstacle to tree establishment can be seed predation. Seed removal (a surrogate of predation) was higher in abandoned slash-and-burn farms than in adjacent forest in the upper Río Negro, Venezuela (Uhl, 1987). Nepstad et al. (1996) also reported in Paragominas, Brazil, higher rates of seed removal by ants and rodents (>80% removal within 20 days for six out of 11 tree species examined) in abandoned pasture than in adjacent forest. In their study, the probability of seed arrival into pastures was higher for smaller-seeded species, but the probability of seed predation in the pasture was lower for larger-seeded species. Therefore, small-seeded species were not as dispersal limited as large-seeded species, but these on the contrary, had a greater chance of getting established. In contrast, Holl and Lulow (1997) observed no obvious correlation between seed size and seed removal rates in an abandoned pasture in Costa Rica. This discrepancy is perhaps due both to differences in community composition of seed predators between localities, and to differences in the extent of site degradation and type of plant cover. Thus, the net effect in predation rates between pasture and adjacent forest microhabitats appears site-specific: for a suite of tree species in each of the following studies, Aide and Cavelier (1994) found higher seed removal in forest, Nepstad et al. (1996) found the opposite trend, while Holl and Lulow (1997) detected no major differences between both microhabitats. At any rate, it seems that most studies carried out so far in the Neotropics on early forest succession have focused mostly at the seed level. To our knowledge, no studies have been designed to determine how species-specific differences in arrival time, substrate preferences for germination, seedling susceptibility to browsing and competing vegetation, as well as among-species differences in seed crop size and sapling height growth rates, can help to predict observed floristic patterns and vertical stratification at later stages (see De Steven, 1991a,b; Palik and Pregitzer, 1991, 1993, for studies in temperate forests).

5. Processes that occur after initial colonization

5.1. Abiotic influences over forest recovery

5.1.1. Light environments and forest succession

Light availability is a crucial abiotic resource that affects plant establishment and growth in moist and wet tropical forests (Denslow, 1987). While understory light environments of Neotropical primary forests are well studied (Chazdon and Fetcher, 1984; Smith et al., 1992; Clark et al., 1996), less is known about their characteristics in secondary stands. Light may not be a limiting factor for early plant establishment in recently abandoned areas but in young stands, light limitation in the understory is expected to be high due to the formation of a dense canopy. At intermediate stages, and because secondary stands generally are even-aged, one would expect their canopies to be fairly homogeneous with few, small-sized gaps. In fact, the canopies of secondary forest stands in Costa Rica and Panamá had a higher frequency of understory microsites at intermediate light levels than old-growth stands which in turn, showed relatively more both low- and high-light microsites (Nicotra et al., 1999; Denslow and Guzman, 2000), although average light availability was similar among stand types. Yet, these studies found no conclusive evidence that reported differences in spatial heterogeneity in understory light microsites among stand types influence seedling species richness as hypothesized previously (Orians, 1982; Denslow, 1987). Because both studies were limited to a single period of data collection, canopy dynamism (i.e., opening and subsequent filling of canopy gaps) may obscure any attempt to confirm this hypothesis.

It appears that after a few decades after site abandonment, rates of treefall gap formation greatly increase in neotropical secondary forests due to canopy senescence of early colonizing tree species as noted by Saldarriaga et al. (1988) in Northern Amazonia. Yavitt et al. (1995) quantified gap occurrence over 10 years in a secondary stand in Barro Colorado Island, Panamá. At the time the observations were initiated, the forest was 60 years old and no gaps were present in their 1.5 ha study plot. However, rates of gap formation and gap size had increased consistently over time. If similar patterns are found in other Neotropical locations, it would suggest that invasion of later plant colonists could be indeed suppressed or at least slowed down for many years probably due to light limitation. Gaps, however, also create soil disturbances and affect belowground processes (Ostertag, 1998) and thus the potential effects of these changes on species replacement also needs to be considered.

The species that dominate the canopies of secondary forests may also affect light availability and further affect successional trajectories. In Costa Rica, Kabakoff and Chazdon (1996) found that due to differences in crown architecture, understory microsites in secondary stands dominated by the canopy tree, *Pentaclethra macroloba* (Mimosoideae) had higher light availability than those beneath *Goethalsia meiantha* (Tiliaceae) trees (see Canham et al., 1994 for a temperate-zone example). Understory composition, such as high abundance of shrubs reported in some secondary stands (Guariguata et al., 1997; Laska, 1997) may also affect tree seedling establishment due to shading and belowground competition (Denslow et al., 1991; Putz and Canham, 1992; Hill et al., 1995).

5.1.2. Development and maintenance of soil properties

While light has been demonstrated to be extremely important to plant establishment in closed-canopy tropical forests, soil properties are also likely to affect the growth and species composition of colonists on deforested land. Many dramatic changes in soil properties occur after deforestation and the burning that often accompanies it (Table 3). One of the most significant impacts is the loss of soil structure, as evidenced by increases in bulk density and decreases in soil porosity. A variety of chemical changes also occur after land conversion, but it is more difficult to generalize about the directionality of these processes. Of the changes described in Table 3, the loss of soil organic matter (SOM) can be particularly detrimental because SOM stabilizes soil aggregates, increases the water-holding capacity of soils, and serves as an energy source for soil decomposers; SOM also influences soil fertility by (1) holding onto organic forms of nutrients and (2) its high cation exchange capacity (CEC). A high CEC facilitates nutrient uptake by allowing cations adsorbed to the soil or SOM to be easily replaced by other cations in solution (Brady, 1990). However, a high CEC is not always beneficial to tropical forest ecosystems. For example, after deforestation and burning CEC can be increased (e.g., Nye and Greenland, 1964; Ewel et al., 1981; Eden et al., 1991; Martins et al., 1991), but these additional base-forming cations on the soil exchange sites can be highly susceptible to leaching loss (Allen, 1985). Thus, in the long-term, deforestation can increase soil acidity and reduce soil fertility.

Additionally, the role of nitrogen in secondary succession deserves special attention because of its potential for loss in tropical ecosystems (Vitousek and Matson, 1988; Vitousek et al., 1989). During land clearing, N is lost mainly through biomass removal, volatilization during burning, denitrification, and leaching (Robertson, 1984; Keller et al., 1993). However, N levels in the soil can be increased after deforestation. For example, after felling and burning Costa Rican pre-montane wet forest, NO_3 and NH_4 levels increased and persisted for 6 months at levels much higher than adjacent secondary forest (Matson et al., 1987). This increase in N pools was due to a 2–3-fold increase in N mineralization, the microbial processing of N from organic to inorganic forms (Matson et al., 1987). Similarly, N mineralization and nitrification rates were higher in slash-and-burn sites than in undisturbed rain forest in Venezuela (Montagnini and Buschbacher, 1989). What may be unique in Neotropical forests is that increases in N mineralization

Table 3
Changes in biological, chemical, and physical soil properties that can occur immediately after deforestation

Soil property	Response	Examples
Bulk density	Increase	Allen (1985), Eden et al. (1991), Martins et al. (1991), Raich (1983), Reiners et al. (1994), Neill et al. (1997)
Soil pH	Increase	Allen (1985), Martins et al. (1991), Ewel et al. (1981), Reiners et al. (1994)
	Decrease	Silver et al. (1996)
Soil porosity	Decrease	Chauvel et al. (1991), Reiners et al. (1994)
Soil organic matter	Decrease	Raich (1983), Weaver et al. (1987), Eden et al. (1991), Martins et al. (1991), Tiessen et al. (1994)
Soil carbon (C)	Decrease	Allen (1985), Raich (1983)
Total nitrogen (N)	Decrease	Allen (1985)
Ammonium (NH_4)	Increase	Matson et al. (1987), Reiners et al. (1994), Silver et al. (1996)
	Decrease	Silver et al. (1996)
Nitrate (NO_3)	Increase	Matson et al. (1987), Silver et al. (1996)
	Decrease	Reiners et al. (1994)
Microbial biomass N	Decrease	Matson et al. (1987)
Nitrogen oxide emissions	Increase	Matson et al. (1987), Keller et al. (1993)
Available phosphorus (P)	No change	Allen (1985)
Extractable P	Increase	Silver et al. (1996)
Exchangeable calcium (Ca)	Increase	Allen (1985), Silver et al. (1996)
	No change	Reiners et al. (1994)
Exchangeable magnesium (Mg)	Increase	Silver et al. (1996)
	Decrease	Allen (1985)
	No change	Reiners et al. (1994)
Exchangeable potassium (K)	Increase	Reiners et al. (1994), Silver et al. (1996)
	No change	Allen (1985)
Exchangeable aluminum (Al)	Decrease	Silver et al. (1996)
Cation exchange capacity (CEC)	Increase	Nye and Greenland (1964), Ewel et al. (1981), Eden et al. (1991), Martins et al. (1991)
	No change	Allen (1985), Reiners et al. (1994)

may be shorter-lived but of a much greater magnitude than those of temperate forests (Matson et al., 1987).

The amount of nutrients in the soil can change over the course of succession, but levels in the soil are generally higher than in plant tissues, and thus the soil provides an important nutrient capital for regrowth after forest clearance (Brown and Lugo, 1990a). As secondary vegetation develops the amount of nutrients in the soil at any given time will be a balance between the (1) storage of nutrients in biomass, (2) turnover and decomposition of the biomass which adds nutrients to the soil, and (3) leaching of nutrients out of the zones accessible by plant roots. Thus, some studies note increases in soil nutrients with forest age (Lamb, 1980; Williams-Linera, 1983; Werner, 1984; Silver et al., 1996), while others note decreases (Uhl and Jordan, 1984). As an example, Hughes et al. (1999) found that the pools of C, N, and S in the soil were relatively stable in a 50-year forest chronosequence in Mexico, despite the fact that pools in aboveground biomass were steadily increasing over time. In another forest chronosequence study in Costa Rica, a 10–20-year-old secondary forest did not differ from primary forest in net N-mineralization rates or net nitrification rates (Reiners et al., 1994). Thus, changes in soil nutrient pools or fluxes over successional time are not always apparent, but there are also numerous differences among these studies in analytical methodology as well. Overall, the recovery of soil to its previous functions varies with forest type (Brown and Lugo, 1990b), soil type (see Allen, 1985; Weaver et al., 1987; Neill et al., 1997, for examples), and the type and intensity of past land use (Buschbacher et al., 1988; Neill et al., 1997). For instance, secondary forests that were formerly pastures have a faster recovery of soil carbon than former agricultural fields (Weaver et al., 1987; Silver et al., 2000). In turn, former agricultural fields subjected to fertilization may have greater amounts of nutrients than secondary forests that regrew after other land uses (Brown and Lugo, 1990b). Despite these variations, once plants begin to colonize a site through the processes described before, a variety of soil–plant feedback processes facilitate the recovery of soil functions.

5.1.3. Role of nutrient availability on forest structure and composition

Aboveground microhabitat differences influence early plant composition during secondary succession (Uhl et al., 1981) but also small-scale variation in soil nutrients has the potential to affect the distribution, composition, and growth of colonizing species. Harcombe (1977) examined successional trajectories over 1 year in fertilized vs. unfertilized plots in a humid tropical forest in Costa Rica. Herbs (that suppressed other life forms) dominated fertilized plots, while shrubs and trees dominated unfertilized plots during the same time period. In the Venezuelan Amazon, Uhl (1987) also found that fertilization exacerbated the dominance of grasses and forbs. Similarly, Huston (1982) concluded experimentally that species dominance during succession may be altered by nutrient availability. In his study, an early successional tree species, *Hampea appendiculata* dominated fertilized plots while in the absence of nutrient additions, its relative abundance was shared with other tree species. All these observations suggest that both floristic and life-form composition during secondary forest succession are influenced by the availability of soil resources. Species with high growth rates may be disproportionately favored under ample resource levels which leads to their overdominance during early succession because slow-growing species tend to be less responsive to enhanced resource levels (Chapin et al., 1986). However, the species composition of a site is not only influenced by soil resources: it also can affect the availability of these resources to other species and thus further affect successional trajectories. This was hypothesized to occur after the exotic nitrogen fixer tree, *Myrica faya*, invaded open sites in Hawaii (Vitousek and Walker, 1989).

At the local and regional level, differences in soil fertility may greatly influence the rate of recovery of forest structure. Tucker et al. (1998) compared successional vegetation (up to 15 years after abandonment) in two study areas in Eastern Amazonia with contrasting soil fertility (Altamira: nutrient-rich Alfisols, and Igarapé-Açu: nutrient-poor Oxisols). Consistently taller canopies (an indicator of fertile soils) were found for all forest age classes within Altamira sites, and tree basal area was also higher. As Fig. 1 suggests, compared to old-growth forest values in their respective locations, recovery of basal area from secondary forests located on recent, nutrient-rich soils appears to proceed faster than in sites of similar age since abandonment on highly weathered, nutrient-poor soils. At the stand level, local variation in soil fertility can affect not only structure but also the distribution of tree species as found in old-growth forests (e.g., Clark et al., 1998). In a 28-year-old secondary forest that developed after pasture abandonment in northeastern Costa Rica, Herrera and Finegan (1997) reported contrasting spatial distributions of the two dominant canopy tree species. Individuals of *Vochysia ferruginea* concentrated on steeper slopes with acid soils, while individuals of *Cordia alliodora* were more abundant on gentler topography with more basic soils. Moreover, these within-stand differences in canopy dominants were found to significantly influence understory floristic composition and species richness (Finegan and Delgado, 2000). Management for timber in secondary forests that show contrasting canopy species distributions should take into account the possibility of tree-by-site preferences when implementing silvicultural prescriptions aimed at regenerating a future stand.

5.2. Recovery of species richness and composition

Under light-to-moderate land use intensity, and when seed sources are nearby, (woody) plant species richness rapidly increases during the first years of secondary forest succession, and it takes no more than a few decades after abandonment to reach values comparable to old-growth forest (Fig. 2). However, as intensity of past land use increases, slower recovery of species richness is expected due to soil compaction, propagule dispersal limitation, and fire occurrence (Uhl et al., 1988; Nepstad et al., 1990, 1996).

Plant size class needs to be taken into account when examining recovery of species richness during succession, because richness and abundance are positively correlated (Denslow, 1995; Condit et al., 1996). Thus, species richness in secondary stands tends to be more

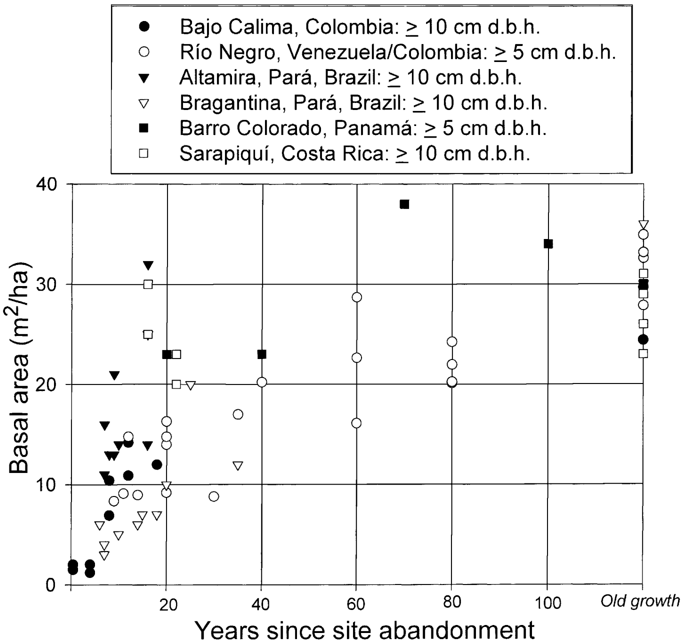

Fig. 1. Basal area accumulation during secondary forest succession in different moist and wet lowland Neotropical localities with light-to-moderate land use intensity before site abandonment. Sources as follows: Bajo Calima (Entisols): Faber-Langendoen (1992); Río Negro (old Oxisols): Saldarriaga et al. (1988); Altamira (Alfisols): Tucker et al. (1998); Bragantina (old Oxisols): Tucker et al. (1998); Barro Colorado (recent Oxisols and Alfisols): Denslow and Guzman (2000); Sarapiquí (recent Ultisols and Inceptisols): Guariguata et al. (1997), Guillén (1993), Lieberman and Lieberman (1994).

similar to old-growth forest when dealing with smaller (i.e., more abundant per unit area) than larger size classes. Saldarriaga et al. (1988) found that in slash-and-burn sites in the upper Rio Negro basin of Venezuela and Colombia, at least 40 years were required for species richness of stems ≥10 cm DBH to attain similar values to that of mature forest, although species richness recovered much more rapidly (between 10 and 20 years) in smaller (>1 cm DBH) individuals. Similarly, in 16–18-year-old secondary forests that regrew in moderately used pastures in Costa Rica, plant species richness was much lower than that of old-growth forest for stems ≥10 cm DBH, but comparable in smaller-sized stems (Guariguata et al., 1997). In a replicated forest chronosequence in central Panamá, Denslow and Guzman (2000) also reported no obvious variation in species richness of woody seedlings as a function of stand age compared to old-growth levels. In subtropical Puerto Rico, plant species richness of woody stems ≥1 cm DBH in abandoned pastures was similar to that of old-growth forest but not before 40 years after abandonment (Aide et al., 1996), an estimate slightly higher than those mentioned above. The fact that plant species richness in small size classes rapidly reaches old-growth forest values in all these studies mentioned, also suggests unlimited propagule dispersal from nearby sources.

While plant species richness in secondary forests can approach old-growth values within a few decades after site abandonment, returning to a species composition similar to old-growth forest will be a much longer process, particularly for canopy trees due to their slow turnover time (Finegan, 1996). This hypothesis is based on long-aged chronosequence studies (Saldarriaga et al., 1988; Denslow and Guzman, 2000) in which the canopy composition after 80–100-years of succession is still not similar to old-growth forest. This time frame will vary considerably depending on forest type, type and intensity of past land use, and environmental conditions. In montane forests, e.g., recovery of canopy composition with respect to old-growth forest may be reached much more rapidly than

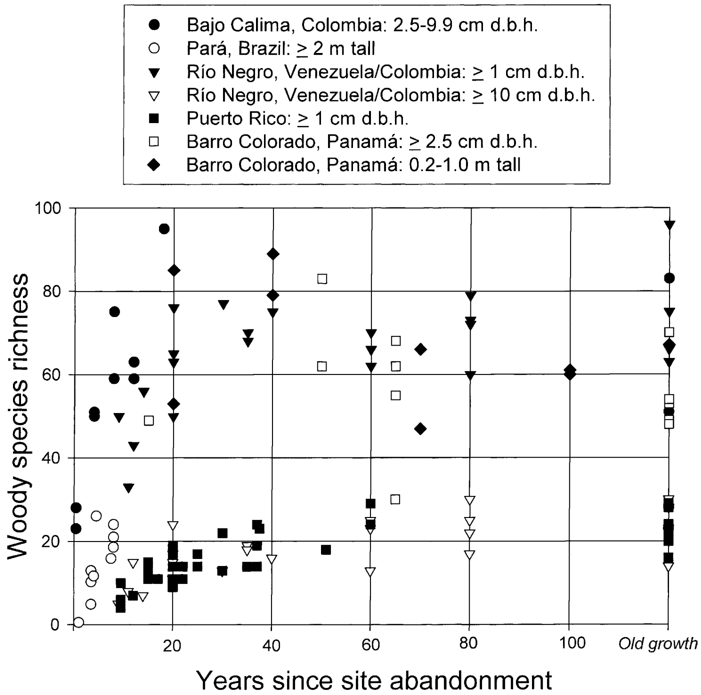

Fig. 2. Woody species richness accumulation during secondary forest succession in different moist and wet lowland Neotropical localities with light-to-moderate land use intensity before site abandonment. Sources as follows: Bajo Calima: Faber-Langendoen (1992); Pará: Uhl et al. (1988); Río Negro: Saldarriaga et al. (1988); Puerto Rico: Aide et al. (1996), Rivera and Aide (1998); Barro Colorado: Knight (1975), for stems ≥2.5 cm d.b.h.; Denslow and Guzman (2000). Due to between-study differences in sampled area and plant size class, data should be compared only within studies with respect to old-growth conditions.

at lower elevations (Byer and Weaver, 1977; Sudgen et al., 1985; Weaver, 1990; Olander et al., 1998). In upland Costa Rica (2900–3000 m a.s.l.), Kappelle et al. (1996) examined changes in forest structure and floristic composition on sites that had been cut, burned, and grazed. The dominant tree species of old-growth (*Quercus copeyensis*, *Q. costaricensis*, and *Weinmannia pinnata*) were already present in 8–20-year-old stands, with comparable relative densities to those of old-growth forest. In contrast, no dominant tree species were shared between old-growth forest and eight, 9–20-year-old stands after abandonment of slash-and-burn agriculture in Amazonia (Saldarriaga et al., 1988). Although more comparative data are needed to verify this observation, an inherently depauperate tree species richness in montane forests as compared to their lowland counterparts (Grubb et al., 1963; Lieberman et al., 1996) may be partially responsible: there are fewer "players" available for site colonization. In fact, Lugo and Scatena (1995) demonstrated that in the Luquillo Mountains of Puerto Rico, the number of successional pathways is reduced with increases in elevation.

Past land use intensity not only affects the rate of species accumulation after site abandonment, but also the composition of early colonizers. In wet Costa Rica, e.g., when land abandonment immediately follows forest cutting (minimal use) there tends to be a notable reduction in abundance of typical short-lived pioneer tree species such as *Cecropia*, *Heliocarpus*, *Ochroma*, and *Trichospermum*. Instead, tree community composition is dominated from the outset by light-demanding but longer-lived species (Guillén, 1993; Hartshorn and Hammel, 1994; Guariguata, 1999). The absence of exposed mineral soil, and the presence of residual vegetation and litter (that is not eliminated by burning), may make it difficult for very small-seeded, short-lived pioneers to germinate and establish (e.g., Uhl et al., 1981; Putz, 1983; Williams-Linera, 1990; Molofsky and Augspurger, 1992). Indirect evidence for this hypothesis comes from the Luquillo Mountains of Puerto Rico, where *Cecropia* appears unable to colonize abandoned pastures the first decades post-abandonment (Aide et al., 1996), in spite of being the most common tree invader after landslides (Brokaw, 1998).

The type of past land use may also affect floristic composition following abandonment. Zimmerman et al. (1995) found in the Luquillo Mountains of Puerto Rico that in 60-year-old abandoned coffee vs. abandoned pasture sites, tree and shrub species diversity was similar but floristic composition was nevertheless greatly different, and that even a strong hurricane that had affected the forest 5 years earlier was not able to erase the effect of land use type on species composition. Also in Puerto Rico but in a geologically different (karst) zone, Rivera and Aide (1998) reported that secondary forests on abandoned pasture sites had similar species richness in comparison with those on abandoned coffee sites, but that compositional differences were marked among these land use types. In lowland Costa Rica, Fernandes and Sanford (1995) found that in abandoned cacao (*Theobroma cacao*) and palm orchards (*Bactris gasipaes*), 30 and 35 tree species dominated these sites, respectively, but only nine of these were common to both. Differences in land use type and intensity can also affect not only species composition but vegetation structure as well. In Eastern Amazonia (*Altamira*), Moran et al. (1996) point out that 82% of the observed statistical variation in tree height was explained by land use type (crop, pasture, crop/pasture). In contrast, Purata (1986) found in Veracruz, Mexico, that length of crop period (i.e., intensity of land use) and not type of land use per se (maize, coffee, pasture) appeared to have the strongest influence on vegetation structure (measured as canopy height and canopy cover). We should point out, however, that intensity, type of land use, and site characteristics are all linked, and therefore difficult to unequivocally separate as single factors.

Besides consideration of individual species, differences in the relative composition of plant life-forms in successional forests to that of old-growth can also have implications for ecosystem functioning (see discussion in Ewel and Bigelow, 1996). For example, Guariguata et al. (1997) found that compared to nearby old-growth stands, abundance of canopy palms in northeastern Costa Rica was much lower in 16–18-year-old secondary stands. Therefore, it would be expected for these particular stands to have lower rates of mechanical damage to saplings by falling palm fronds (Vandermeer, 1977; Clark and Clark, 1991), and perhaps differences in the hydrological and nutrient budgets as palms channel more rainfall toward their stem than dicotyledonous trees (Enright, 1987). Fast-growing tree species in successional forests may also show lower damage and mortality rates than their old-growth counterparts not only because of stand age but due to their low propensity of liana infestation (Putz, 1984; Clark and Clark, 1990).

The question of how important regaining the original species composition is for determining the functions of the forest is still an important but understudied topic. There is some evidence that similar ecosystem level processes occur during secondary succession, regardless of the number or composition of species present. After forest felling and burning, Ewel et al. (1991) created successional communities including (1) successional vegetation that colonized on its own, (2) an imitation of natural succession in which the species planted were physiognomically similar but not floristically similar to natural succession, and (3) an enriched succession in which at least 20 additional species not native to the study site were introduced monthly. Over a 5-year period, these successional communities did not differ in their nutrient retention properties, but soil nutrients did decline beneath all treatments over time. Species richness also did not affect rates of herbivory; leaf area loss was similar among monocultures and these successional communities even though herbivory rates varied among species (Brown and Ewel, 1987). These experiments indicate that during secondary succession, the ability of species to occupy a site and use resources may be as important as the composition and diversity of species that colonize an area, but studies during the later stages of succession are clearly needed.

5.3. Accumulation of biomass

Typically, secondary forest succession is characterized by shifts in the biomass allocation of the plant community (Ewel, 1971). In early succession, relatively more biomass is allocated to resource acquiring tissues (leaves and fine roots) and in later stages more is allocated towards structural materials (woody stems and coarse roots). Fine root (<2 mm diameter) biomass accumulates at a slower rate than leaf biomass, but its recovery can still be quite rapid. Secondary forests can have greater fine root biomass than plantations of similar age (Cuevas et al., 1991). Secondary forests can also have similar or higher fine root biomass than old-growth forest after 1 year (Raich, 1980, 1983), 6 years (Ewel, 1971), or 10 year post-abandonment (Cavelier et al., 1996). Fine root length densities (cm root/cm^3 of soil) in 15 year secondary forest can be higher than in old-growth forest in eastern Amazonia (da Oliveira Carvalheiro and Nepstad, 1996). These recovery times for fine root biomass in secondary forests are similar to ones after natural disturbances (Parrotta and Lodge, 1991; Silver and Vogt, 1993), but not all sites may recover fine root biomass as quickly (Silver et al., 1996).

As root biomass recovers, it is hypothesized that vesicular-arbuscular mycorrhizal communities will also recover. There are few experimental investigations of mycorrhizal associations during secondary succession, although land conversion to pasture may decrease fungal densities (Allen et al., 1998) or affect mycorrhizal propagules (Fischer et al., 1994). In Venezuelan páramo, 1-year-old fallow plots had much lower percentage of roots with infection and extra-matrical mycelia, but fallow land that was 6- and 9-year-old had higher levels of these variables (Montilla et al., 1992). The recovery of either mycorrhizal community structure or function is virtually unknown, but has been hypothesized to affect succession by allowing some species to persist and dominate presumably due to their ability to tolerate various soil conditions (Janos, 1980).

Aboveground biomass recovery of secondary forests is well studied in secondary forests (see Brown and Lugo, 1990a). Secondary forests are generally sinks of biomass as they re-vegetate, and thus they are also sinks of atmospheric carbon (Lugo and Brown, 1992). In general, secondary forests rapidly accumulate up to 100 t/ha of biomass for about 15–20 years after abandonment (Brown and Lugo, 1990a; Silver et al., 2000). When a variety of studies are considered together, aboveground biomass usually shows an asymptotic pattern with time, although factors such as climate and past land use (Brown and Lugo, 1990a; Silver et al., 2000) tend to affect the rate of accumulation. Secondary forests that originated after shifting cultivation grow faster than secondary forests developing in abandoned pastures (Fearnside and Guimaraes, 1996). Over the first 20 years, Silver et al. (2000) found that dry forests accumulated biomass faster than moist or wet forests. Over an 80-year time span, however, moist forests accumulated biomass at the fastest rate. It is possible that differing regeneration mechanisms may lead to these patterns; e.g., if resprouting is common it is likely to lead to a faster rate of initial biomass accumulation than regeneration by seed.

However, the time it takes for secondary forests to reach biomass resembling old-growth forests is still unknown. Brown and Lugo (1990b) concluded that after 80 years biomass was not comparable to old-growth, while Hughes et al. (1999) did not find comparable aboveground biomass and carbon values to old-growth even after 50 years of secondary succession in a wet forest in Mexico. Most likely, aboveground biomass will not resemble old-growth conditions until the appearance of very large trees, which sequester a much larger proportion of total biomass (Brown and Lugo, 1992; Clark and Clark, 1996). Differences in the rate of maximum biomass accumulation after site abandonment may also be obvious among localities. Along a forest chronosequence in Central Panamá, Denslow and Guzman (2000), reported a peak in tree basal area at intermediate (70 year) stand ages, followed by a decline in 100-year old stands, to eventually reach somewhat lower, old-growth values. In contrast, 80-year-old secondary forests at oligotrophic sites in the Venezuelan and Colombian Amazon (Saldarriaga et al., 1988), showed that basal area (and aboveground biomass) was still asymptotic to old-growth values (see Fig. 1). Because both sites had similar rainfall patterns, variation in site productivity may account for such differences (Denslow, 2000).

5.4. Net primary productivity and nutrient cycling

In general, secondary forests can be highly productive, which is why they are often suggested as good timber sources. In early forest development (e.g., <20 years), leaf litter production, represents more of the total net primary productivity than wood production. Productivity of wood can be low until leaf and root systems are fully developed, but after this period short-term estimates of wood production can be higher than estimates for old-growth forests (Brown and Lugo, 1990a).

Productivity and nutrient cycling are invariably linked because as plant tissues grow they sequester nutrients and as these tissues die they return some of the nutrients to the soil. The vegetation of secondary forests serves as a nutrient sink that quickly accumulates biomass and nutrients into leaves and roots during approximately the first 15 years of succession (Brown and Lugo, 1990a). Such rapid nutrient accumulation is accompanied by fast rates of nutrient turnover (e.g., high rates of litterfall and fast leaf decomposition rates) that can be more rapid than plantations (Lugo, 1992) or other land uses. As forests age, however, most of the biomass is allocated to woody tissue and the turnover rate of nutrients decrease (Brown and Lugo, 1990a). These decreases in nutrient turnover rates can be due to (1) lower concentrations of nutrients in plant tissues, (2) lower rates of organic matter input, and (3) decreased rates of litter decomposition in the soil (Vitousek et al., 1989; Mesquita et al., 1998). Thus, the general pattern of nutrient cycling in secondary forests appears to be fast rates of nutrient accumulation in leaves and roots and fast turnover of these nutrients during the early portions of succession, and a shift to slower rates of nutrient turnover during the later stage of succession. While land use history, climate, and soil type certainly affect the rates of these processes, the same basic pattern of nutrient cycling appears to be occurring in many secondary forests (Brown and Lugo, 1990a).

6. Conclusions

The regenerative power of Neotropical forest vegetation is clearly high, if propagule sources and land use intensity before abandonment has not been severe. Nonetheless, the recovery of biophysical properties and vegetation is heavily dependent on the interactions between site-specific factors and land use, which makes it extremely difficult to predict successional trajectories in anthropogenic settings. Considerations of site history have provided many useful insights into how Neotropical forest structure and function is influenced by human activity (e.g., Garcia-Montiel and Scatena, 1994; Foster et al., 1999), but as yet we are unable to develop a deterministic model of how land use history and intensity affects tropical forests. In fact, although we tend to understand the processes of secondary forest succession (or at least the ones that might be important), we often cannot predict the patterns of species replacement due to these interacting factors. This realization is counter to most ecological thinking, where the search for pattern is used to form hypotheses about the processes that generate these patterns.

Despite the difficulty in predicting species replacement patterns, we hypothesize that there is a sequence of events and processes that occurs during secondary succession, regardless of the species composition (Table 4). This sequence begins with initial site colonization, progresses through canopy closure, recovery of species richness, increases in basal area and biomass, and ends with a return to a species composition similar to old-growth conditions. During early stages of succession, factors governing site colonization (e.g., seed dispersal, biophysical characteristics, remnant vegetation) are very important. After canopy closure, nutrient cycling rates and productivity tend to be high, until biomass and basal area begin to level off, but not reach old-growth conditions. After natural gap formation starts in the forest, long-lived pioneers dominate the canopy, the appearance of very large trees leads to aboveground biomass values similar to old-growth conditions, and productivity tends to asymptote. We hypothesize that this sequence of events occurs in all successions, and suggest that many forest functions and characteristics may resemble old-growth conditions long before species composition does. This hypothesis raises many questions such as the length of time it takes for a forest to return to previous rates of desired ecosystem services, and how these rates are affected by past land use history, environmental conditions, and present management practices. These questions are important not only for those trying to restore tropical forests but also for those interested in production purposes. As we have shown throughout this review, integrating the structural and functional characteristics of secondary succession should enhance our ability both to predict and manage successional forest ecosystems.

Table 4

A conceptual model showing a hypothesized sequence for the processes occurring during secondary forest succession, in reference to old-growth conditions. The crux of the model is that overstory species composition resembles old-growth conditions as the last step in the sequence; other forest characteristics or processes may resemble old-growth much earlier. The times are meant to be a guide to the time scale of these processes, but these are based on very limited empirical data

Process	Canopy vegetation	Time scale (years)	Notes
Initial colonization	Grass, herbs, ferns	1–5	Factors that affect initial colonization include: 1. Landscape features (distance to forest, topography) 2. Climate and microclimate 3. Presence/absence of past vegetation (seed bank, resprouts, remnant trees and shrubs) 4. Site characteristics (nutrient availability, soil compaction, mycorrhizae, type and intensity of past land use) 5. Multi-species interactions (seed predation, herbivory, perch availability, pathogens, competition, phenological stage)
Early forest development	Short-lived pioneers	5–20	Early stages of forest development include: 1. Canopy closure 2. Fine root biomass levels become similar to mature forest 3. Stemflow and throughfall levels become similar to mature forest 4. High rates of litterfall, NPP, and turnover of nutrients 5. Rapid accumulation of biomass, along with self-thinning and the appearance of standing dead 6. Accumulation of species, and the possibility that understory species richness is similar to mature forest
Late forest development	Long-lived pioneers	20–100	Later stages of forest development include: 1. More frequent small-scale disturbances, particularly small canopy gaps 2. Prevalence of advanced regeneration 3. Greater storage of nutrients in biomass, perhaps lower rates of NPP and litterfall 4. Low spatial heterogeneity in understory light levels
Old-growth forest	Shade-tolerant trees	100–400	Old-growth forest characterized by: 1. Very diverse overstory tree species composition 2. Prevalence of large canopy gaps, other chronic disturbances 3. Very large trees 4. High spatial heterogeneity in understory light levels

Acknowledgements

We thank M. Aide, J. Denslow, A. Lugo, J. Putz, and F. Scatena for their comments on various iterations of the ideas presented here. MRG acknowledges the Agencia Suiza para el Desarrollo y la Cooperación (COSUDE) through the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) for financial support.

References

Alvarez-Buylla, E., Martinez-Ramos, M., 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. Oecologia 84, 314–325.

Aide, T.M., Cavelier, J., 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. Restoration Ecol. 2, 219–229.

Aide, T.M., Zimmerman, J.K., Rosario, M., Marcano, H., 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in Northeastern Puerto Rico. Biotropica 28, 537–548.

Allen, J.C., 1985. Soil response to forest clearing in the United States and the tropics: geological and biological factors. Biotropica 17, 15–27.

Allen, E.B., Rincon, E., Allen, M.F., Perez-Jimenez, A., Huante, P., 1998. Disturbance and seasonal dynamics of mycorrhizae in a tropical deciduous forest in Mexico. Biotropica 30, 261–274.

Brady, N.C., 1990. The Nature and Properties of Soils, 10th Edition. Macmillan, New York, 621 pp.

Brokaw, N.V.L., 1998. *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. Bot. Rev. 64, 91–120.

Brokaw, N.V.L., Grear, J.S., 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. Biotropica 23, 386–392.

Brown, B.J., Ewel, J.J., 1987. Herbivory in complex and simple tropical successional ecosystems. Ecology 68, 108–116.

Brown, S., Lugo, A.E., 1990a. Tropical secondary forests. J. Trop. Ecol. 6, 1–32.

Brown, S., Lugo, A.E., 1990b. Effects of forest clearing and succession on the carbon and nitrogen content of soils in Puerto Rico. Plant and Soil 124, 53–64.

Brown, S., Lugo, A.E., 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17, 8–18.

Budowski, G., 1961. Studies on forest succession in Costa Rica and Panama. Ph.D. Dissertation. Yale University, New Haven, CT, p. 189.

Buschbacher, R., Uhl, C., Serrão, E.A.S., 1988. Abandoned pastures in Eastern Amazonia. II. Nutrient stocks in the soil and vegetation. J. Ecol. 76, 682–699.

Bush, M.B., Colinvaux, P.A., 1994. Tropical forest disturbance: paleoecological records from Darién, Panamá. Ecology 75, 1761–1768.

Byer, M.D., Weaver, P.L., 1977. Early secondary succession in an elfin woodland in the Luquillo Mountains of Puerto Rico. Biotropica 9, 35–47.

Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. 24, 337–349.

Cavelier, J., Estevez, J., Arjona, B., 1996. Fine root biomass in three successional stages of an Andean cloud forest in Colombia. Biotropica 28, 728–736.

Chapin, F.S., Vitousek, P.M., Van Cleeve, K., 1986. The nature of nutrient limitation in plant communities. Am. Naturalist 127, 48–58.

Chauvel, A., Grimaldi, M., Tessier, D., 1991. Changes in soil pore-space distribution following deforestation and revegetation: an example from the Central Amazon Basin, Brazil. For. Ecol. Mgmt. 38, 259–271.

Chazdon, R.L., Coe, F.G., 1999. Ethnobotany of woody species in second growth, old-growth, and selectively logged forests of Northeastern Costa Rica. Conserv. Biol. 13, 1312–1322.

Chazdon, R.L., Fetcher, N., 1984. Photosynthetic light environments in a lowland tropical forest in Costa Rica. J. Ecol. 72, 553–564.

Cheke, A.S., Nanakorn, W., Yankoses, C., 1979. Dormancy and dispersal of secondary forest species under the canopy of a primary tropical rain forest in Northern Thailand. Biotropica 11, 88–95.

Clark, D.B., 1996. Abolishing virginity. J. Trop. Ecol. 12, 735–739.

Clark, D.B., Clark, D.A., 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. J. Trop. Ecol. 6, 321–331.

Clark, D.B., Clark, D.A., 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. J. Ecol. 79, 447–457.

Clark, D.B., Clark, D.A., 1996. Abundance, growth, and mortality of very large trees in neotropical lowland rain forest. For. Ecol. Mgmt. 80, 235–244.

Clark, D.B., Clark, D.A., Rich, P.M., Weiss, S., Oberbauer, S., 1996. Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. Can. J. For. Res. 26, 747–757.

Clark, D.B., Clark, D.A., Read, J.M., 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. J. Ecol. 86, 101–112.

Condit, R., Hubbell, S.P., LaFrankie, J.V., Sukumar, R., Manokaran, N., Foster, R.B., Ashton, P.S., 1996. Species-area and species individual relationships for tropical trees: a comparison of three 50-ha plots. J. Ecol. 84, 549–562.

Corlett, R.T., 1994. What is secondary forest? J. Trop. Ecol. 10, 445–447.

Cuevas, E., Brown, S., Lugo, A.E., 1991. Above- and belowground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. Plant and Soil 135, 257–268.

Dalling, J.W., Denslow, J.S., 1998. Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panamá. J. Veg. Sci. 9, 669–678.

Dalling, J.W., Swaine, M.D., Garwood, N.C., 1997. Soil seed bank dynamics in seasonally moist lowland tropical forest, Panamá. J. Trop. Ecol. 13, 659–680.

Dalling, J.W., Swaine, M.D., Garwood, N.C., 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecology 79, 564–578.

da Oliveira Carvalheiro, K., Nepstad, D.C., 1996. Deep soil heterogeneity and fine root distribution in forests and pastures of eastern Amazonia. Plant and Soil 182, 279–285.

da Silva, J.M.C., Uhl, C., Murray, G., 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned amazonian pastures. Conserv. Biol. 10, 491–503.

Denevan, W.M., 1992. The pristine myth: the landscape of the Americas in 1492. Ann. Assoc. Am. Geographers 82, 369–385.

Denslow, J.S., 1987. Tropical rainforest gaps and species diversity. Ann. Rev. Ecol. Systematics 18, 431–452.

Denslow, J.S., 1995. Disturbance and diversity in tropical rain forests: the density effect. Ecol. Appl. 5, 962–968.

Denslow, J.S., 2000. Patterns of structure and diversity across a tropical moist forest chronosequence. J. Veg. Sci., in press.

Denslow, J.S., Newell, E., Ellison, A.M., 1991. The effect of understory palms and cyclanths on the growth and survival of *Inga* seedlings. Biotropica 23, 225–234.

Denslow, J.S., Guzman, S., 2000. Variation in stand structure, light, and seedling abundance across a tropical moist forest chronosequence. Panama. J. Veg. Sci. 11, 201–212.

De Steven, D., 1991a. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology 72, 1066–1075.

De Steven, D., 1991b. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72, 1076–1088.

Dupuy, J.M., Chazdon, R.L., 1998. Long-term effects of forest regrowth and selective logging on the seed bank of tropical forests in NE Costa Rica. Biotropica 30, 223–237.

Eden, M.J., Furley, P.A., McGregor, D.F.M., Milliken, W., Ratter, J.A., 1991. Effect of forest clearance and burning on soil properties in northern Roraima, Brazil. For. Ecol. Mgmt. 38, 283–290.

Enright, N.J., 1987. Stemflow as a nutrient source for nikau palm (*Rhopalostylis sapida*) in a New Zealand forest. Aust. J. Ecol. 12, 17–24.

Ewel, J.J., 1971. Biomass changes in early tropical succession. Turrialba 21, 110–112.

Ewel, J.J., 1976. Litterfall and leaf decomposition in a tropical forest succession in Eastern Guatemala. J. Ecol. 64, 293–308.

Ewel, J.J., Bigelow, S.W., 1996. Plant life forms and tropical ecosystem functioning. In: Orians, G.H., Dirzo, R., Cushman, H. (Eds.), Biodiversity and Ecosystem Processes in Tropical Forests. Springer, Berlin, pp. 101–126.

Ewel, J.J., Berish, C., Brown, B., Price, N., Raich, J., 1981. Slash and burn impacts on a Costa Rican wet forest site. Ecology 62, 816–829.

Ewel, J.J., Mazzarino, M.J., Berish, C.W., 1991. Tropical soil fertility changes under monocultures and successional communities of different structure. Ecol. Appl. 1, 289–302.

Faber-Langendoen, D., 1992. Ecological constraints on rain forest management at Bajo Calima, Western Colombia. For. Ecol. Mgmt. 53, 213–244.

Fearnside, P.M., Guimaraes, W.M., 1996. Carbon uptake by secondary forests in Brazilian Amazonia. For. Ecol. Mgmt. 80, 35–46.

Fernandes, D.N., Sanford, R.L., 1995. Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. Conserv. Biol. 9, 915–922.

Fimbel, R.A., Fimbel, C.C., 1996. The role of exotic conifer plantations in rehabilitating degraded tropical forest lands: a case study from the Kibale Forest in Uganda. For. Ecol. Mgmt. 81, 215–226.

Finegan, B., 1992. The management potential of neotropical secondary lowland rain forest. For. Ecol. Mgmt. 47, 295–321.

Finegan, B., 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. Trends Ecol. Evol. 11, 119–124.

Finegan, B., Delgado, D., 2000. Structural and floristic heterogeneity in a Costa Rican rain forest restored on pasture through natural secondary succession. Restoration Ecol., in press.

Fischer, C.R., Janos, D.P., Perry, D.A., Linderman, R.G., Sollins, P., 1994. Mycorrhiza inoculum potentials in tropical secondary succession. Biotropica 26, 369–377.

Foster, D.R., Fluet, M., Bose, E.R., 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. Ecol. Appl. 9, 555–572.

Fu, S., Rodriguez Pedraza, C., Lugo, A.E., 1996. A twelve-year comparison of stand changes in a mahogany plantation and a paired natural forest of similar age. Biotropica 28, 515–524.

Garcia-Montiel, D.C., Scatena, F.N., 1994. The effect of human activities on the structure and composition of a tropical forest in Puerto Rico. For. Ecol. Mgmt. 63, 57–78.

Garwood, N.C., 1989. Tropical soil seed banks: a review. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Banks. Academic Press, San Diego, CA, pp. 149–209.

Garwood, N.C., Janos, D.P., Brokaw, N.V.L., 1979. Earthquake-caused landslides: a major disturbance to tropical forests. Science 205, 997–999.

George, S.J., Kumar, B.M., Rajiv, G.R., 1993. Nature of secondary succession in the abandoned *Eucalyptus* plantations of Neyyar (Kerala) in peninsular India. J. Trop. For. Sci. 5, 372–386.

Gómez-Pompa, A., Vázquez-Yanes, C., 1976. Estudios sobre sucesión secundaria en los trópicos cálido-húmedos: el ciclo de vida de las especies secundarias. In: Gómez-Pompa, A., Vázquez-Yanes, C., Del Amo, S.R., Butanda, C.A. (Eds.), Regeneración de Selvas. Compañía Editorial Continental, Mexico, pp. 579–593.

Gorchov, D.L., Cornejo, F., Ascorra, C., Jaramillo, M., 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio 107/108, 339–349.

Grubb, P.J., Lloyd, J.T., Pennington, T.D., Whitmore, T.C., 1963. A comparison of lowland and montane forests in Ecuador. I. The forest structure, physiognomy, and floristics. J. Ecol. 51, 567–601.

Guariguata, M.R., 1999. Early response of selected tree species to liberation thinning in a young secondary forest in Northeastern Costa Rica. For. Ecol. Mgmt. 124, 255–261.

Guariguata, M.R., 2000. Seed and seedling ecology of tree species in neotropical secondary forests: management implications. Ecol. Appl. 10, 145–154.

Guariguata, M.R., Rheingans, R., Montagnini, F., 1995. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. Restoration Ecol. 3, 252–260.

Guariguata, M.R., Chazdon, R.L., Denslow, J.S., Dupuy, J.M., Anderson, L., 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecol. 132, 107–120.

Guevara, S., Laborde, J., 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Vegetatio 107/108, 319–338.

Guevara, S., Meave del Castillo, J., Moreno-Casasola, P., Laborde, J., 1992. Floristic composition and vegetation structure under isolated trees in neotropical pastures. J. Veg. Sci. 3, 655–664.

Guillén, L., 1993. Inventario comercial y analisis silvicultural de bosques humedos secundarios en la region Huetar Norte de Costa Rica. Thesis. Instituto Tecnologico de Costa Rica, Cartago, Costa Rica.

Harcombe, P.A., 1977. The influence of fertilization on some aspects of succession in a humid tropical forest. Ecology 58, 1375–1383.

Harrington, R.A., Ewel, J.J., 1997. Invasibility of tree plantations by native and non-indigenous plant species in Hawaii. For. Ecol. Mgmt. 99, 153–162.

Hartshorn, G.S., Hammel B., 1994. Vegetation types and floristic patterns. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A., Hartshorn, G.S. (Eds.), La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago, USA, pp. 73–89.

Harvey, C.A., 2000. Windbreaks enhance seed dispersal into agricultural landscapes in Monteverde, Costa Rica. Ecol. Appl. 10, 155–173.

Herrera, B., Finegan, B., 1997. Substrate conditions, foliar nutrients and the distributions of two canopy tree species in a Costa Rican secondary rain forest. Plant and Soil 191, 259–267.

Hill, J.D., Canham, C.D., Wood, D.M., 1995. Patterns and causes of resistance to tree invasion in rights-of-way. Ecol. Appl. 5, 459–470.

Holl, K.D., 1998. Do bird perching structures elevate seed rain and establishment in abandoned tropical pasture? Restoration Ecol. 6, 253–261.

Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31, 229–242.

Holl, K.D., Lulow, M.E., 1997. Effects of species, habitat, and distance from edge on post-dispersal seed predation in a tropical rain forest. Biotropica 29, 459–468.

Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region in Mexico. Ecology 80, 1892–1907.

Huston, M.A., 1982. The effect of soil nutrient and light on the growth and interactions during tropical forest succession: experiments in Costa Rica. Ph.D. Dissertation. University of Michigan, MI.

Hutchinson, I.D., 1993. Silvicultura y manejo en un bosque secundario tropical: caso Pérez-Zeledón, Costa Rica. Revista Forestal Centroamericana 2, 13–18.

Janos, D.P., 1980. Mycorrhizae influence tropical succession. Biotropica 12 (Suppl.), 56–64.

Kabakoff, R.P., Chazdon, R.L., 1996. Effects of canopy species dominance on understory light availability in low-elevation secondary forest stands in Costa Rica. J. Trop. Ecol. 12, 779–788.

Kammesheidt, L., 1998. The role of tree sprouts in the restoration of stand structure and species diversity in tropical moist forest after slash-and-burn agriculture in Eastern Paraguay. Plant Ecol. 139, 155–165.

Kammesheidt, L., 1999. Forest recovery by root suckers and above-ground sprouts after slash-and-burn agriculture, fire and logging in Paraguay and Venezuela. J. Trop. Ecol. 15, 143–157.

Kappelle, M., Geuze, T., Leal, M., Cleef, A.M., 1996. Successional age and forest structure in a Costa Rican upper montane *Quercus* forest. J. Trop. Ecol. 12, 681–698.

Keenan, R., Lamb, D., Woldring, O., Irvine, T., Jensen, R., 1997. Restoration of plant biodiversity beneath tropical tree plantations in Northern Australia. For. Ecol. Mgmt. 99, 117–131.

Keller, M., Veldkamp, E., Weitz, A.M., Reiners, W.A., 1993. Effect of pasture age on soil trace-gas emissions from a deforested area of Costa Rica. Nature 365, 244–246.

Kenoyer, L.A., 1929. General and successional ecology of the lower tropical rain-forest at Barro Colorado Island, Panama. Ecology 10, 210–222.

Knight, D.H., 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. Ecol. Monographs 45, 259–284.

Kuusipalo, J., Adjers, G., Jafarsidik, Y., Antii, O., Tuomela, K., Vuokko, R., 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: understory development in forest plantations. J. Veg. Sci. 6, 205–210.

Lamb, D., 1980. Soil nitrogen mineralization in secondary rainforest succession. Oecologia 47, 257–263.

Lamb, D., Parrota, J., Keenan, R., Tucker, N., 1997. Rejoining habitat remnants: restoring degraded rainforest lands. In: Laurance, W.F., Bierregaard Jr., R.O. (Eds.), Tropical Forest Remnants. University of Chicago Press, Chicago, IL, pp. 366–385.

Lang, G.E., Knight, D.H., 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. Ecology 64, 1075–1080.

Laska, M.S., 1997. Structure of understory shrub assemblages in adjacent secondary and old-growth tropical wet forests, Costa Rica. Biotropica 29, 29–37.

Lieberman, M., Lieberman, D., 1994. Patterns of density and dispersion of forest trees. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A., Hartshorn, G.S. (Eds.), La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago, IL, pp. 106–119.

Lieberman, D., Lieberman, M., Peralta, R., Hartshorn, G.S., 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. J. Ecol. 84, 137–152.

Lugo, A.E., 1992. Comparison of tropical tree plantations and with secondary forests of similar age. Ecol. Monographs 62, 1–41.

Lugo, A.E., 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. For. Ecol. Mgmt. 99, 9–19.

Lugo, A.E., Brown, S., 1992. Tropical forests as sinks of atmospheric carbon. For. Ecol. Mgmt. 54, 239–255.

Lugo, A.E., Scatena, F.N., 1995. Ecosystem-level properties of the Luquillo Experimental Forest with emphasis on the tabonuco forest. In: Lugo, A.E., Lowe, C. (Eds.), Tropical Forests: Management and Ecology. Springer, New York, pp. 59–108.

Martins, P.F. da S., Cerri, C.C., Volkoff, B., Andreux, F., Chauvel, A., 1991. Consequences of clearing and tillage on the soil of a natural Amazonian ecosystem. For. Ecol. Mgmt. 38, 273–302.

Matson, P.A., Vitousek, P.M., Ewel, J.J., Mazzarino, M.J., 1987. Nitrogen transformations following tropical forest felling and burning on a volcanic soil. Ecology 68, 491–502.

Mesquita, R. de C.G., Workman, S.W., Neely, C.L., 1998. Slow litter decomposition in a *Cecropia*-dominated secondary forest of Central Amazonia. Soil Biol. Biochem. 30, 167–175.

Mizrahi, A., Ramos Prado, J.M., Jimenez-Osorio, J., 1997. Composition, structure, and management potential of secondary dry tropical vegetation in two abandoned henequen plantations of Yucatan, Mexico. For. Ecol. Mgmt. 96, 273–282.

Molofsky, J., Augspurger, C.K., 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73, 68–77.

Montagnini, F., Buschbacher, R., 1989. Nitrification rates in two undisturbed tropical rain forests and three slash-and-burn sites of the Venezuelan Amazon. Biotropica 21, 9–14.

Montilla, M., Herrera, R.A., Monasterio, M., 1992. Micorrizas vesiculo-arbusculares en parcelas que se encuentran en sucesion-regeneracion en los Andes tropicales. Suelo y Planta 2, 59–70.

Moran, E.F., Packer, A., Brondizzio, E., Tucker, J., 1996. Restoration of vegetation cover in the Eastern Amazon. Ecol. Econ. 18, 41–54.

Müller, E., 1998. Land use policy and secondary forest management in the northern zone of Costa Rica. In: Guariguata, M.R., Finegan, B. (Eds.), Ecology and Management of Tropical Secondary Forest: Science, People, and Policy. Reuniones Técnicas No. 4, Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica, pp. 11–18.

Murcia, C., 1997. Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forests in Colombia. For. Ecol. Mgmt. 99, 163–170.

Neill, C., Melillo, J.M., Steudler, P.A., Cerri, C.C., de Moraes, J.F.L., Piccolo, M.C., Brito, M., 1997. Soil carbon and nitrogen stocks following forest clearing for pasture in the southwestern Brazilian Amazon. Ecol. Appl. 7, 1216–1225.

Nepstad, D.C., Uhl, C., Serrao, E.A., 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Para, Brazil. In: Anderson, A.B. (Ed.), Alternatives to Deforestation. Columbia University Press, New York, pp. 215–229.

Nepstad, D.C., Uhl, C., Pereira, C.A., da Silva, J.M.C., 1996. A comparative study of tree establishment in abandoned pasture and mature forest of Eastern Amazonia. Oikos 76, 25–39.

Nicotra, A.B., Chazdon, R.L., Iriarte, S.V.B., 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. Ecology 80, 1908–1926.

Nye, P.H., Greenland, D.J., 1964. Changes in the soil after clearing tropical forest. Plant and Soil 21, 101–112.

Olander, L.P., Scatena, F.N., Silver, W.L., 1998. Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. For. Ecol. Mgmt. 109, 33–49.

Orians, G.H., 1982. The influence of tree-falls in tropical forests on tree species richness. Trop. Ecol. 23, 255–279.

Ostertag, R., 1998. Belowground effects of canopy gaps in a tropical wet forest. Ecology 79, 1294–1304.

Palik, B.J., Pregitzer, K.S., 1991. The relative influence of establishment time and height-growth rates on species and vertical stratification during secondary forest succession. Can. J. For. Res. 21, 1481–1490.

Palik, B.J., Pregitzer, K.S., 1993. The vertical development of early successional forests in northern Michigan, USA. J. Ecol. 81, 271–285.

Parrotta, J.A., 1992. The role of plantation forests in rehabilitating degraded ecosystems. Agric. Ecosyst. Environ. 41, 115–133.

Parrotta, J.A., Knowles, O.H., 1999. Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. Restoration Ecol. 7, 103–116.

Parrotta, J.A., Lodge, D.J., 1991. Fine root dynamics in a subtropical wet forest following hurricane disturbance in Puerto Rico. Biotropica 23, 343–347.

Powers, J.S., Haggar, J.P., Fisher, R.F., 1997. The effect of overstory composition on understory woody regeneration and species richness in 7-year-old plantations in Costa Rica. For. Ecol. Mgmt. 99, 43–54.

Purata, S.E., 1986. Floristic and structural changes during old-field succession in the Mexican tropics in relation to site history and species availability. J. Trop. Ecol. 2, 257–276.

Putz, F.E., 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64, 1069–1074.

Putz, F.E., 1984. The natural history of lianas on Barro Colorado Island, Panamá. Ecology 65, 1713–1724.

Putz, F.E., Canham, C.D., 1992. Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. For. Ecol. Mgmt. 49, 267–275.

Quintana-Asencio, P.F., Gonzalez-Espinosa, M., Ramirez-Marcial, N., Dominguez-Vazquez, G., Martinez-Ico, M., 1996. Soil seed banks and regeneration of tropical rain forest from milpa fields at the Selva Lacandona, Chiapas, Mexico. Biotropica 28, 192–209.

Raich, J.W., 1980. Fine roots regrow rapidly after forest felling. Biotropica 12, 231–232.

Raich, J.W., 1983. Effects of forest conversion on the carbon budget of a tropical soil. Biotropica 15, 177–184.

Raich, J.W., Gong, W.K., 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. J. Trop. Ecol. 6, 203–217.

Reiners, W.A., Bouwman, A.F., Parsons, W.F.J., Keller, M., 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. Ecol. Appl. 4, 363–377.

Rico-Gray, V., Garcia-Franco, J., 1992. Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. J. Veg. Sci. 3, 617–624.

Rivera, L.W., Aide, T.M., 1998. Forest recovery in the karst region of Puerto Rico. For. Ecol. Mgmt. 108, 63–75.

Robertson, G.P., 1984. Nitrification and nitrogen mineralization in a lowland rainforest succession in Costa Rica, Central America. Oecologia 61, 99–104.

Saldarriaga, J.G., West, D.C., Tharp, M.L., Uhl, C., 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. J. Ecol. 76, 938–958.

Salo, J., Kalliola, R., Hakkinen, I., Makinen, Y., Niemela, P., Puhakka, M., Coley, P.D., 1986. River dynamics and the diversity of Amazon lowland forest. Nature 322, 254–258.

Silver, W.L., Vogt, K.A., 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. J. Ecol. 81, 729–738.

Silver, W.L., Scatena, F.N., Johnson, A.H., Siccama, T.G., Watt, F., 1996. At what temporal scales does disturbance affect below-ground nutrient pools? Biotropica 28, 441–457.

Silver, W.L., Ostertag, R., Lugo, A.E., 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restoration Ecol., in press.

Smith, A.P., Hogan, K.P., Idol, J.R., 1992. Spatial and temporal patterns of light and canopy structure in a lowland tropical moist forest. Biotropica 24, 503–511.

Smith, J., Sabogal, C., de Jong, W., Kaimowitz, D., 1998. Secondary forests as a resource for promoting rural development and environmental conservation in the tropics of Latin America. Occasional Paper No. 13. Center for International Forestry Research, Bogor, Indonesia.

Snedaker, S.C., 1970. Ecological studies on tropical moist forest succession in eastern lowland Guatemala. Ph.D. Dissertation. University of Florida, Gainesville, FL.

Standley, P.C., 1937. Flora of Costa Rica. Field Museum of Natural History Botanical Series No. 392. Chicago, IL.

Sudgen, A.M., Tanner, E.V.J., Kapos, V., 1985. Regeneration following clearing in a Jamaican montane forest: results of a ten-year study. J. Trop. Ecol. 1, 329–351.

Terborgh, J., Weske, J.S., 1969. Colonization of secondary habitats by Peruvian birds. Ecology 50, 765–782.

Tergas, L.E., Popenoe, H.C., 1971. Young secondary vegetation and soil interactions in Izabal, Guatemala. Plant and Soil 34, 675–690.

Thomlinson, J.R., Serrano, M.I., del M. López, T., Aide, T.M., Zimmerman, J.K., 1996. Land-use dynamics in a post-agriculture Puerto Rican landscape (1936–1988). Biotropica 28, 525–536.

Tiessen, H., Cuevas, E., Chacon, P., 1994. The role of organic matter in sustaining soil fertility. Nature 371, 783–785.

Toledo, V.M., Batis, A.I., Becerra, R., Martinez, E., Ramos, C.H., 1995. La selva util: etnobotanica cuantitativa de los grupos indigenas del tropico humedo de Mexico. Interciencia 20, 177–187.

Tucker, J., Brondizzio, E.S., Moran, E.F., 1998. Rates of forest regrowth in Eastern Amazonia: a comparison of Altamira and Bragantina regions, Para State, Brazil. Interciencia 23, 1–10.

Uhl, C., 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J. Ecol. 75, 377–407.

Uhl, C., Clark, K., 1983. Seed ecology of selected Amazon Basin successional species. Bot. Gazette 144, 419–425.

Uhl, C., Jordan, C.F., 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology 65, 1476–1490.

Uhl, C., Clark, K., Clark, H., Murphy, P., 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. J. Ecol. 69, 631–649.

Uhl, C., Jordan, C., Clark, K., Clark, H., Herrera, R., 1982. Ecosystem recovery in Amazon caatinga forest after cutting, cutting and burning, and bulldozer clearing treatments. Oikos 38, 313–320.

Uhl, C., Buschbacher, R., Serrao, E.A.S., 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. J. Ecol. 76, 663–681.

Vandermeer, J., 1977. Notes on density dependence of *Welfia georgii* Wendl. ex Burret (Palmae), a lowland rainforest species in Costa Rica. Brenesia 10/11, 9–15.

Vázquez-Yanes, C., Orozco-Segovia, A., 1994. Signals for seeds to sense and respond to gaps. In: Caldwell, M.M., Pearcy, R.W. (Eds.), Exploitation of Environmental Heterogeneity by Plants. Academic Press, San Diego, CA, pp. 209–236.

Vieira, I.C.G., Uhl, C., Nepstad, D., 1994. The role of the shrub *Cordia multispicata* Cham. as a ‘‘succession facilitator’’ in an abandoned pasture, Paragominas, Amazonia. Vegetatio 115, 91–99.

Vitousek, P.M., Matson, P.A., 1988. Nitrogen transformations in a range of tropical forest soils. Soil Biol. Biochem. 20, 361–368.

Vitousek, P.M., Walker, L.R., 1989. Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. Ecol. Monographs 59, 247–266.

Vitousek, P.M., Matson, P.A., Van Cleve, K., 1989. Nitrogen availability and nitrification during succession: primary, secondary, and old-field seres. Plant and Soil 115, 229–239.

Voeks, R.A., 1996. Tropical forest healers and habitat preference. Econ. Bot. 50, 381–400.

Wadsworth, F.H., 1997. Forest production for tropical America. Agriculture Handbook 710. United States Department of Agriculture Forest Service, Washington, DC, p. 563.

Walker, B.H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6, 18–23.

Walker, L.R., Chapin III, F.S., 1987. Interactions among processes controlling successional change. Oikos 50, 131–135.

Weaver, P.L., 1990. Succession in the elfin woodland of the Luquillo Mountains of Puerto Rico. Biotropica 22, 83–89.

Weaver, P.L., Birdsey, R.A., Lugo, A.E., 1987. Soil organic matter in secondary forests of Puerto Rico. Biotropica 19, 17–23.

Werner, P., 1984. Changes in soil properties during tropical wet forest succession in Costa Rica. Biotropica 16, 43–50.

Williams-Linera, G., 1983. Biomass and nutrient content in two successional stages of tropical wet forest in Uxpanapa, Mexico. Biotropica 15, 275–284.

Williams-Linera, G., 1990. Origin and early development of forest edge vegetation in Panama. Biotropica 22, 235–241.

Yavitt, J.B., Battles, J.J., Lang, G.E., Knight, D.H., 1995. The canopy gap regime in a secondary neotropical forest in Panama. J. Trop. Ecol. 11, 391–402.

Young, K.R., Ewel, J.J., Brown, B.J., 1987. Seed dynamics during forest succession in Costa Rica. Vegetatio 71, 157–173.

Zimmerman, J.K., Aide, T.M., Rosario, M., Serrano, M., Herrera, L., 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. For. Ecol. Mgmt. 77, 65–76.