BIOMASS AND NUTRIENT DYNAMICS OF RESTORED NEOTROPICAL FORESTS

ARIEL E. LUGO[1]*, WHENDEE L. SILVER[2] and SANDRA MOLINA COLÓN[3]
[1] *International Institute of Tropical Forestry, USDA Forest Service, Jardín Botánico Sur, 1201 Calle Ceiba, Río Piedras, PR 00926-1119, Puerto Rico;* [2] *Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management, 151 Hilgard Hall 3110, University of California, Berkeley, California 94720, U.S.A.;* [3] *Department of Biology, Pontificia Universidad Católica de Puerto Rico, 2250 Las Américas Suite 570, Ponce, Puerto Rico 00731-6382*
(author for correspondence, e-mail: alugo@fs.fed.us; phone: 787 766 5335; fax: 787 766 6263)*

(Received 20 August 2002; accepted 28 April 2003)

Abstract. Restoring species-rich tropical forests is an important activity because it helps mitigate land deforestation and degradation. However, scientific understanding of the ecological processes responsible for forest restoration is poor. We review the literature to synthesize the current state of understanding of tropical forest restoration from a biogeochemical point of view. Aboveground biomass and soil carbon accumulation of restored tropical forests are a function of age, climate, and past land use. Restored forests in wet life zones accumulate more biomass than those in moist or dry life zones. Forests restored on degraded sites accumulate less aboveground biomass than forests restored on pastures or agricultural land. Rates of aboveground biomass accumulation in restored forests are lower than during natural succession, particularly during the first decades of forest establishment. Rates of litterfall, biomass production, soil carbon accumulation, and nutrient accumulation peak during the first few decades of restored forest establishment and decline in mature stages. Changes in species composition and canopy closure influence the rate of primary productivity of older restored stands. Species composition also influences the rate and concentration of nutrient return to the forest floor. The ratio of primary productivity to biomass is high in young restored forests and low in mature stands irrespective of climate. The ratio is low when past land use has little effect on biomass accumulation, and high when past land uses depresses biomass accumulation. This effect is due to a high rate of litterfall in restored forests, which helps restore soil by circulating more nutrients and biomass per unit biomass accumulated in the stand. The degree of site degradation and propagule availability dictates the establishment and growth of tree species. Reestablishment of forest conditions and the enrichment of sites by plant and animal species invasions lead to faster rates of succession, aboveground primary productivity, and biomass accumulation in restored forests. Our review demonstrates that nutrient cycling pathways and nutrient use efficiency are critical for interpreting the suitability of tree species to different conditions in forest stands undergoing restoration.

Keywords: carbon cycling, Luquillo Experimental Forest, neotropical forest restoration, nutrient cycling, organic matter dynamics, Puerto Rico, tree plantations

1. Introduction

The restoration of tropical forests is a matter of concern due to the importance of maintaining land productivity and sustaining the economies of tropical countries (Brown and Lugo, 1994). We use the term restoration to mean the restoration of

Water, Air, and Soil Pollution: Focus **4:** 731–746, 2004.

forests, irrespective of species composition, on deforested lands by rehabilitating forest conditions and site productivity (Brown and Lugo, 1994). There is a clear tendency in the tropics for addressing the problem of degraded lands through reforestation and afforestation projects. For example, the area of tree plantation in the 90 countries monitored by the Food and Agriculture Organization (FAO, 1993) increased by 150% at an annual rate of 2.6 million ha between 1980 and 1990 and 2.0 million ha a^{-1} between 1990 and 2000 (FAO, 2001b). The purpose of many of these plantations is for land protection or rehabilitation. Numerous literature reports of successes of both small and large-scale restoration projects in the tropics further demonstrate the increasing importance of tropical forest restoration (e.g., Field, 1996; Parrotta and Turnbull, 1997; FAO, 2001a). Nevertheless, the area subjected to restoration and rehabilitation is still small (13%) in comparison to the area deforested annually in the tropics (FAO, 2001b).

There are many techniques for restoring tropical forests, and several authors have reviewed them (e.g., Brown and Lugo, 1994; Parrotta and Turnbull, 1997; Ashton *et al*., 2001). The many techniques for restoring species-rich tropical forests on degraded lands involve two basic approaches. The first approach involves planting one or more tree species, and allowing them to develop into species-rich forests. A second approach is allowing natural regeneration and succession, either accelerated or not by humans, to proceed to mature states. Usually, management objectives, site conditions, and availability of resources determine which approach to use. However, where soil degradation is extreme, as occurs after mining activities, tree planting is required to restore forest conditions because arrested succession prevents natural forest regeneration (Parrotta and Turnbull, 1997).

The scientific understanding of tropical forest restoration lags behind the practice of restoring such forests. Much progress is possible without scientific understanding when restoring tropical forests in deforested lands because tropical succession can rapidly reestablish forest cover on most abandoned sites. However, overcoming arrested succession requires human intervention and technical knowledge to restore forests. The complexity of tropical forests is a major reason for the knowledge gap about their ecology and silviculture. Most of the literature addresses the species aspects of the activity (what species to plant or favor, how to promote or accelerate species richness, how to deal with alien species, etc.) and there is very little work on biogeochemistry. Moreover, it takes about 100 years for planted or fallowed forest stands to reach maturity in the tropics (Brown and Lugo, 1990), and we lack long-term studies of the successional process and biogeochemistry in these systems. As a result, a definitive synthesis of organic matter and nutrient dynamics in restored forests is not possible at this time.

We present case-study information on rates of organic matter and nutrient accumulation of tropical forests that were either restored through planting on degraded lands and allowed to mature as mixed species forests, or restored naturally and matured after abandonment of various types of land use. The case studies include a species-rich forest restored in Puerto Rico through planting on pastures on a

moist site (La Condesa in the Luquillo Experimental Forest, LEF), and species-rich forests restored through both planting and natural succession after abandonment of various land uses on dry (Guánica Forest) and wet (LEF and the Amazon) forest sites. We compare the results from these case studies with forest regeneration (natural and planted) elsewhere in the tropics. Our objective is to identify the range of rate processes associated with restored tropical forests and some of the primary mechanisms that might affect those rates. We ask if rates of organic matter and nutrient dynamics in restored forests are different from rates observed in natural forests of similar age and growing under similar climates and soils.

2. Description of the Study Sites

We use data from three locations: the Colombian and Venezuelan Amazon (Saldarriaga, 1994), the LEF (Lugo *et al*., 1990b; Lugo, 1992; Cuevas and Lugo, 1998), and the Guánica Forest Puerto Rico (Molina Colón, 1998; Lugo and Fu, 2002). Each location had several forest stands. In Colombia and Venezuela, Saldarriaga (1994) described a chronosequence with six age classes of Tierra Firme Forest in the tropical wet lowlands. Stands were naturally recovering from slash and burn agricultural land use. At the LEF, Silver *et al*. (in press) studied the organic matter dynamics of La Condesa, a subtropical moist forest (sensu Holdridge, 1967) planted on degraded pasturelands some 60 years earlier. At the LEF, Lugo (1992) also studied a chronosequence of paired tree plantations and secondary forests established on abandoned agricultural lands in the subtropical wet forest life zone (8 stands). Two plantations were coniferous (*Pinus caribaea*) and two were broad leaved (*Swietenia macrophylla*). In addition, Lugo *et al*. (1990b), and Cuevas and Lugo (1998) studied litter dynamics in 10 tree species planted on abandoned subsistence agricultural lands in the LEF arboretum (Francis, 1989). At Guánica Forest, Molina Colón (1998) studied naturally restored dry forests following abandonment of various land uses (4 stands). She compared these with an adjacent mature dry forest stand. We also present nutrient concentration data for *Swietenia mahagoni* leaves from plantations in Guánica Forest established on sites previously used for agriculture (Lugo and Fu, 2002). We compare these data with unpublished information for leaves of *Dacryodes excelsa*, a primary forest species in the LEF.

In summary, we present data for 22 stands in the three locations (the Amazon, LEF, and Guánica Forest). Seven of the stands were restored through planting and the other 15 were restored through natural regeneration. Stands represent five types of past land uses (farming, pastures, housing, baseball park, and charcoal production), three life zones (dry, moist, and wet), and ranged in age from 4 to about 200 yr.

Because we are reporting data for forest stands that are not in steady state, we cannot estimate the rate of turnover with available data. Instead, we use the ratio of an organic matter production flux (stemwood biomass accumulation, litterfall, or

their sum) to the corresponding biomass at a particular time in the development of the forest. This ratio, expressed in percent per year, is the percentage of standing biomass fixed annually through primary productivity at a given age. The absolute value of this ratio varies with the flux used (stemwood biomass production, litterfall or their sum) and the biomass compartments included in the denominator. For the purpose of this article, we standardized net aboveground primary productivity (NAPP) to mean aboveground stem biomass accumulation plus litterfall. This flux was divided by total live biomass (aboveground plus roots). We also used aboveground stem biomass accumulation rate when litterfall data were not available. In those instances, we divided by the aboveground biomass, which excluded roots. Net primary productivity (NPP) was the sum of aboveground biomass accumulation, litterfall, and root productivity. When NPP data were available, we divided by total live biomass.

3. Organic Matter Dynamics

The pattern of organic matter production and accumulation in secondary tropical forests is well known (Brown and Lugo, 1990). Silver *et al*. (2000) found higher aboveground biomass in reforested tropical systems in wet than in moist or dry life zones. Net primary productivity is higher early in the development of the forest, and declines as it reaches maturity (Figure 1a). Forest biomass accumulates steadily through the life of the forest (Figure 1b). In the absence of disturbances, the forest continues to accumulate biomass as it approaches steady state asymptotically. Old forest stands accumulate most of their biomass in soil and large trees (Brown and Lugo, 1992), tree that are usually absent in young forests, particularly those planted when restoring sites after conversion to non-forest. In some instances, large trees remain on site after land abandonment, and these trees have important ecological functions during forest restoration (Toh *et al*., 1999; Silver *et al*., in press).

An aspect that differentiates restored forests from stands undergoing natural succession is the effect that past land use has on the rate of biomass accumulation (Brown and Lugo, 1990). Silver *et al*. (2000) showed that aboveground biomass production in rehabilitated forests on abandoned land was a function of the type of land degradation. Biomass production was fastest in abandoned agriculture, slower in abandoned pastures, and slowest in cleared land with arrested succession. All of these rates are slower, however, than those measured in natural successions (Aide *et al*., 1995; Silver *et al*., 2000).

We found that ratios of organic matter production to biomass based on NAPP and total biomass were higher than ratios based on aboveground biomass accumulation rate and aboveground biomass (Figure 2). These differences are artifacts of the computation, as both estimates resulted in the same patterns. The pattern of the organic matter production to biomass ratio in restored forests has three characteristics (Figure 2). The ratio is high early after planting or natural regeneration,

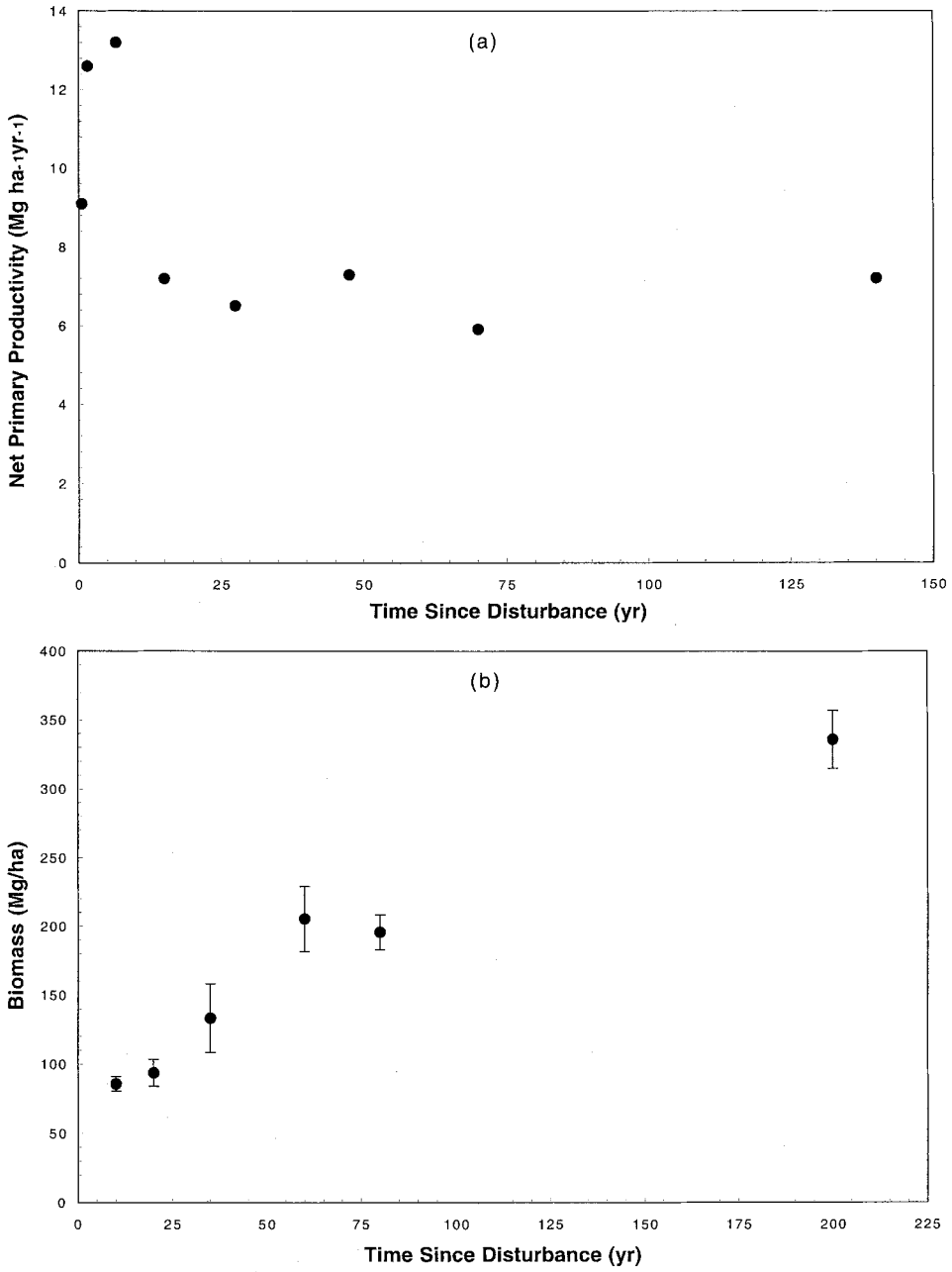

Figure 1. Net primary productivity (a), and total biomass (b) in a chronosequence of sites recovering from agricultural use in Tierra Firme forests of the Colombian and Venezuelan Amazon. Total biomass includes aboveground live and dead aboveground plus roots (100-cm depth), while net productivity includes root productivity. Standard error bars are based on $n = 3$ (age class 60) or 4. All data are from Saldarriaga (1994).

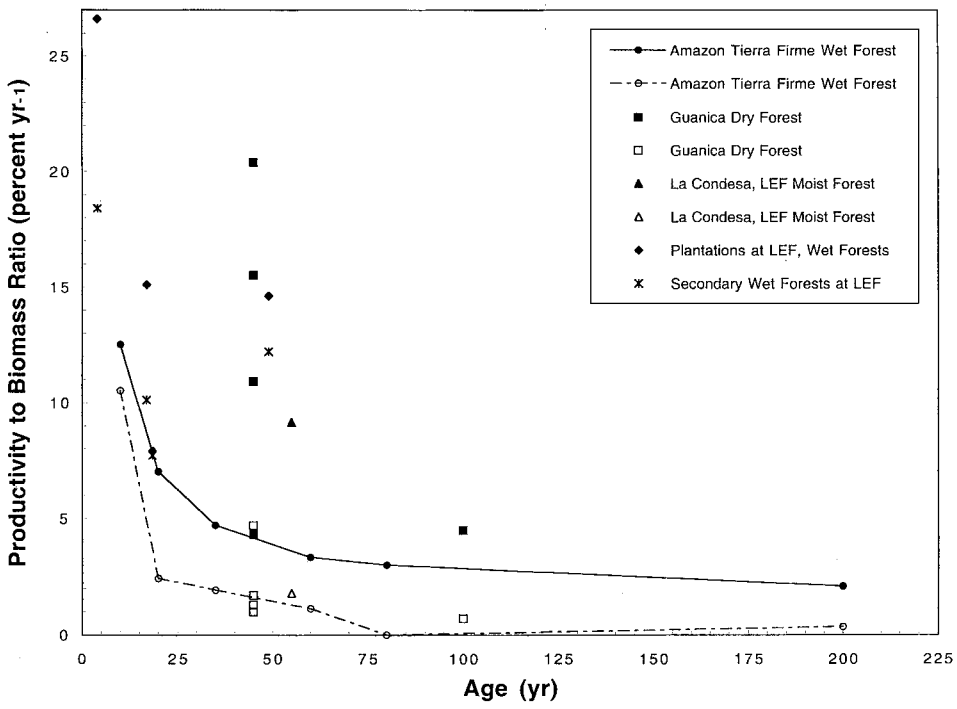

Figure 2. Ratio of net aboveground primary productivity (NAPP) to total biomass (solid line), and ratio of aboveground biomass accumulation rate to aboveground biomass (dotted line). Net aboveground primary productivity is the sum of litter fall rate and aboveground biomass accumulation rate. Total biomass includes aboveground and live root biomass. Aboveground biomass includes stems and leaves. Closed symbols represent ratios of NAPP/total biomass and open symbols represent ratios of aboveground biomass accumulation rate to aboveground biomass. The connected points highlight the chronosequence of Saldarriaga (1994). Other data are from Lugo (1992), Lugo and Murphy (1986), Molina Colón (1998), and Silver *et al.* (in press). Luquillo Experimental Forest is LEF.

and decreases as the forest matures. However, even mature restored forests (La Condesa) had ratios between 2 and 9% a^{-1}. The organic matter production to biomass ratio does not appear to be life-zone-dependent as are the rates of production and biomass accumulation (Brown and Lugo, 1982). Notice for example, that dry forests in Guánica exhibit ratios similar in magnitude to those of the wet and moist forests at LEF or the Amazon.

The dry forest stands in Guánica, each representing a different past land use at age 45 yr, exhibited a wide range in the ratio of organic matter production to biomass, suggesting that the intensity of past land use affects the relation between production and biomass matter. The mechanism is that past land use affected the accumulation of biomass to a higher degree than it did the primary productivity of the site. Those sites with low biomass (former baseball park, houses, and farms) had higher organic matter production to biomass ratios than high biomass charcoal pits and mature forest. The level of litterfall, a major component of primary

TABLE I

Nutrient accumulation (kg ha^{-1}) in vegetation (above and belowground) of various rehabilitated forest stands in Puerto Rico (Lugo, 1992), and mature undisturbed stands of montane rain forests in New Guinea (Edwards and Grubb, 1982). The average aboveground mineral content of four undisturbed mature tropical sites is included for comparison (Edwards, 1982). The age of secondary forests is approximate

Site and age (yr)	N	P	K
Planted stands			
Pinus caribaea (4)	360	13	53
Pinus caribaea (17)	1450	55	514
Swietenia macrophylla (18.5)	565	29	364
Swietenia macrophylla (49)	1001	37	415
Natural regeneration			
Secondary Forest (4 yr)	227	8	165
Secondary Forest (18 yr)	619	35	484
Secondary Forest (17 yr)	498	36	468
Secondary Forest (49 yr)	479	29	369
Undisturbed mature forest			
New Guinea	820	43	854
Four mature tropical forests	1599	92	1218

productivity, was not significantly different among sites (Molina Colón, 1998). Thus, even though a site might not be accumulating much biomass, it could exhibit high productivity and could be transferring organic matter at relatively fast rates, a situation that influences site conditions through soil and litter (Brown and Lugo, 1990).

4. Nutrient Dynamics

Young tree plantations and secondary forests on degraded lands had a lower aboveground nutrient capital than mature undisturbed forests (Table I). Planted forest usually had a larger nutrient pool than secondary forests of similar age and, as they aged, accumulated as much N as undisturbed mature stands (Table I). Planted forests are of known age, so it is possible to estimate a rate of nutrient accumulation in biomass. For those in Table I, the rates of nutrient accumulation decreased

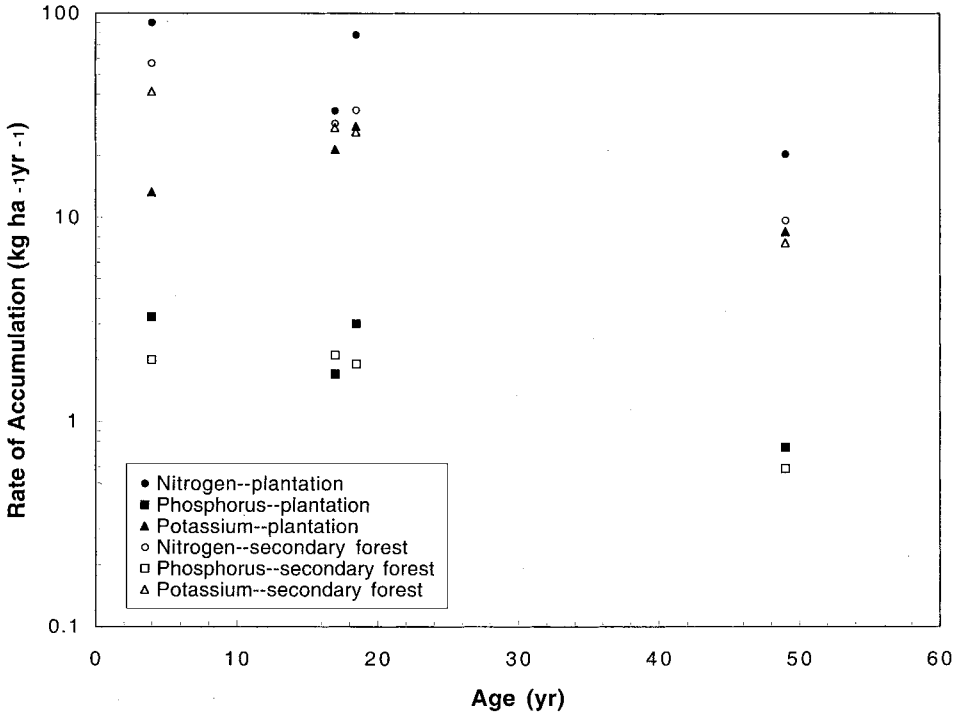

Figure 3. Rate of nutrient accumulation with age in four plantations (solid circles), and four paired secondary forests (open circles) of similar age in the Luquillo Experimental Forest, Puerto Rico Data are derived from Table I.

with age (Figure 3). The reduction in rate was particularly notable in the oldest plantation. For example, the rates of P accumulation (kg ha^{-1} a^{-1}) were 3.3, 3.0, 1.7, and 0.8 for plantations at ages 4, 19, 17, and 49 yr. These dynamics reflect the tendency of trees for high uptake of nutrients from the soil early in their life cycle and to depend on retranslocation during later stages of the life cycle (Bowen and Nambiar, 1984; Attiwill and Leeper, 1987).

Trees 'dilute' their overall initial nutrient capital by increasing organic matter storage at a faster rate than the storage of nutrients. This process allows trees to survive in infertile soils, provided they successfully become established. Increased nutrient retranslocation and recycling with age allows older forest stands to sustain a larger biomass pool with similar or lower soil nutrient uptake as younger stands. This behavior contributes to the function of forests as nutrient and carbon sinks. Sequestration of carbon and nutrients occurs in woody tissue with low nutrient concentration, while production of new tissue uses nutrients acquired by retranslocation and soil uptake.

The key to the success of restored forest function is the capacity of the first tree crop to acquire and concentrate sufficient nutrient capital from the soil to establish forest conditions, i.e., a canopy cover, understory microclimate, and modification

TABLE II

Ratio of annual nutrient return to nutrient accumulation in litter of ten tree species growing as plantations under the same conditions on abandoned agricultural land in the Arboretum of the Luquillo Experimental Forest. Units are in a^{-1} and data for the estimates are from Lugo *et al*. (1990), and Cuevas and Lugo (1998). Species are arranged in rank order of annual litter production rate. Annual litter production rates for species with the same letters are not statistically different at $p < 0.05$

Species	N	P	K	Ca	Mg
Pinus caribaea[a]	0.40	0.45	0.75	0.53	0.66
Hibiscus elatus[a]	1.46	1.75	2.91	1.16	2.13
Eucalyptus saligna[ab]	0.73	0.76	1.43	0.59	1.15
Pinus elliottii[b]	0.30	0.36	0.51	0.32	0.52
Eucalyptus patentinervis[b]	0.82	1.17	1.12	0.46	0.84
Khaya nyasica[b]	0.70	0.84	1.69	0.65	0.93
Swietenia macrophylla[bc]	0.53	0.66	1.27	0.55	0.80
Terminalia ivorensis[bc]	1.70	1.95	2.97	1.29	2.25
Hernandia sonora[bc]	1.59	1.36	2.81	1.90	2.18
Anthocephalus chinensis[c]	0.57	0.83	1.09	0.50	0.72

of soil structure and chemistry. Once forest conditions are established, other tree and non-tree plant and animal species invade the site and succession processes change in response to the biota.

Our research with tree plantations and natural forest stands in Puerto Rico shows that the capacity to acquire soil nutrients from soil, return nutrients via litterfall, accumulate nutrients in soil, and rate of decomposition are species-specific (Frangi and Lugo, 1985; Lugo *et al*., 1990a, b; Wang *et al*., 1991; Cuevas and Lugo, 1998). Others report similar observations on species-specific nutrient dynamics in tropical tree plantations established on degraded lands (Bernhard-Reversat and Loumeto, 2002; Montagnini, 2001, 2002). Table II illustrates species-specific differences in terms of the ratio of nutrients in litterfall to nutrients stored in litter of 23 to 26 yr-old plantations. Three species, *Hibiscus elatus, Terminalia ivorensis*, and *Hernadia sonora* had high ratios for all nutrients, suggesting that the litter of these species recycles nutrients very rapidly. In contrast, *Pinus caribaea* and *Pinus elliottii* consistently had low ratios, suggesting nutrient accumulation in their litter compartment. Other species exhibited variation in the ratios according to the nutrient.

Figure 4 shows a contrasting pattern of nutrient concentration during leaf development and decomposition in *Dacryodes excelsa*, a primary forest species, and *Swietenia mahagoni*, a species used for site restoration in dry climates. Leaves

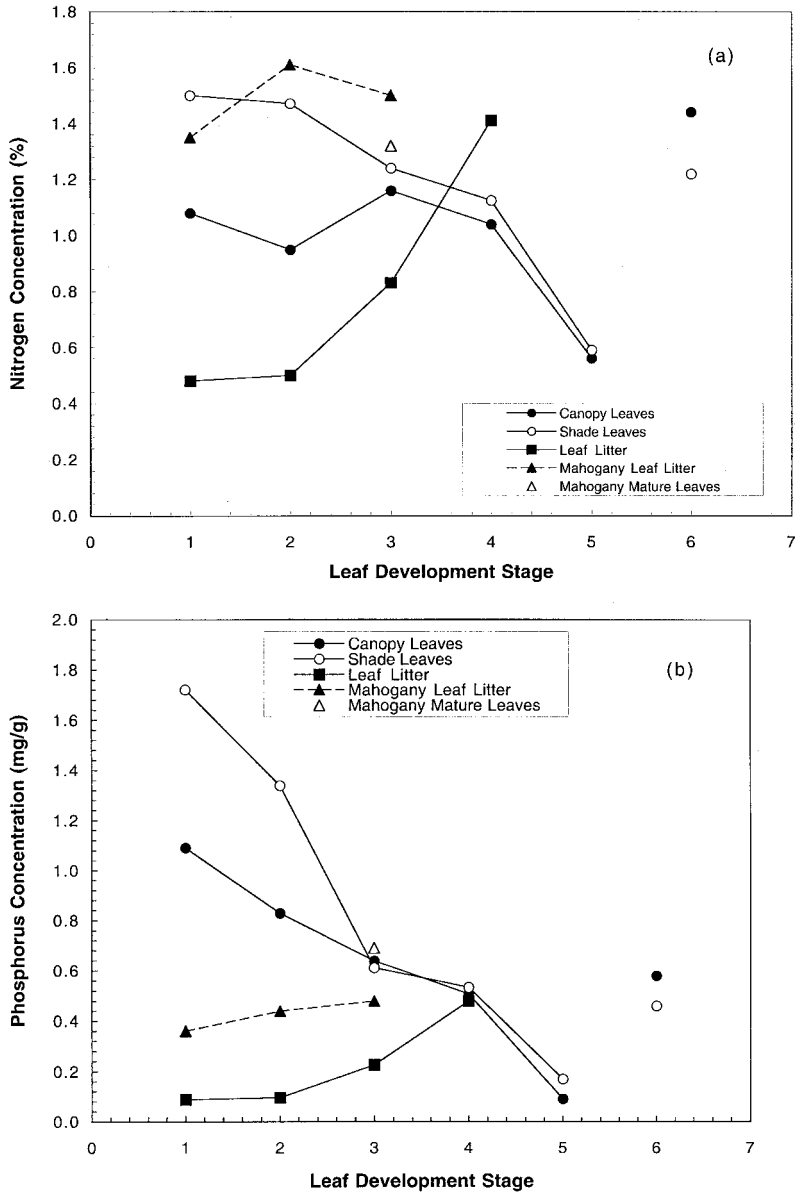

Figure 4. Change in nutrient concentration (N, P, K, and Ca) of leaves and leaf litter of *Dacryodes excelsa* (solid lines) and leaf litter of *Swietenia mahagoni* (dotted lines). Each point represents a different stage of leaf development or decomposition. For canopy and shade leaves, 1 = expanding leaves, 2 = young leaves, 3 = mature leaves, 4 = old leaves, 5 = senescent leaves, and 6 = green leaves blown or knocked down to the forest floor. For *Dacryodes* leaf litter, 1 = yellow leaves, 2 = whole brown leaves, 3 = fragmented brown leaves, and 4 = highly decomposed leaves. For *Swietenia* leaf litter, 1 = recently fallen leaves, 2 = leaves buried half way into the litter layer, and 3 = leaves in the bottom of the litter layer (Lugo and Fu, 2002). Open triangles correspond to the nutrient concentration of mature *Swietenia* leaves (Sánchez *et al*., 1997).

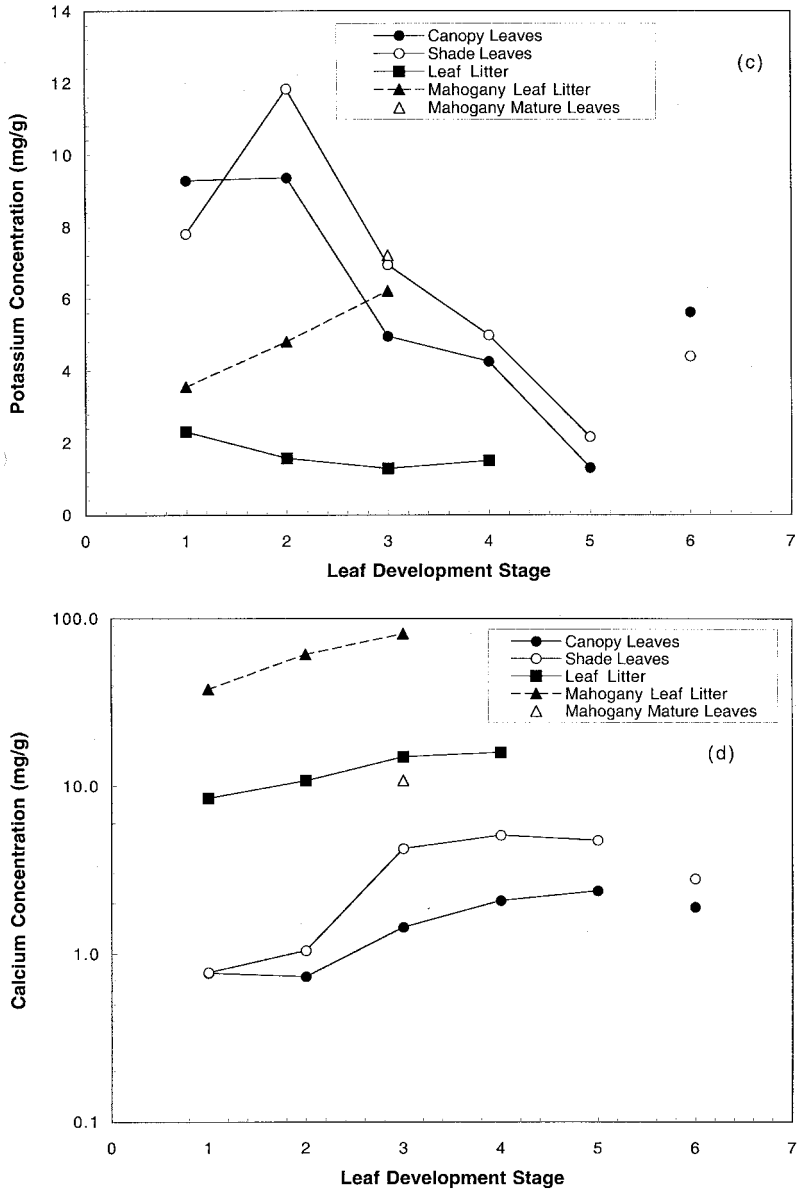

Figure 4. (Continued).

of *Dacryodes* constantly change their nutrient concentration through their development and decomposition stages. Canopy leaves have lower concentrations than shade leaves, but follow the same pattern of reduction in nutrient concentration with age. At the time of leaf fall, the leaf is at its lowest concentration due to retranslocation. Lugo (1992) and Medina and Cuevas (2002) found similar patterns in *Swietenia macrophylla* leaves. Cuevas and Lugo (1998) found that the nutrient

TABLE III

Examples of how tree species influence nutrient cycling attributes of stands. The text contains literature citations with examples

Nutrient cycling attribute	Implications for restoration
Uptake rate	Capacity to grow in the site.
Retranslocation rate	Regulates the quality of litterfall, reduces the uptake requirement.
Return to the forest floor	Opportunity for recycling and improvement of site fertility.
Accumulation in biomass	Sink function and retention of nutrients on site.
Distribution between above and belowground compartments	Determines opportunity for building soil fertility (belowground) vs. circulating nutrients aboveground.
Quality of tissue	Influence on decomposition and consumption rates by fungi, bacteria, and soil organisms.
Efficiency of recycling	High efficiency favors living plants (re use), low efficiency makes more nutrients available for the rest of the system.
Efficiency of storage	High efficiency favors the sink function.
Episodic return	Introduces pulses of nutrient availability.
Episodic retranslocation	Causes periodic changes in the quality of litterfall.
Episodic mast production	Can dominate the nutrient return pathway and favor particular nutrient cycling pathways.
Episodic change in use efficiency	Causes periodic changes in the quality of plant tissue.

concentration in leaf litterfall of mahogany and other species changed throughout the year, thus causing temporal change in the quality of fresh litter.

During decomposition, nutrient concentrations increased to levels similar to those of mature leaves (Figure 4). Leaves that fall green have higher nutrient concentration than senescent leaves. In comparison with *Dacryodes, Swietenia* leaves exhibit higher nutrient concentrations throughout their decomposition stages, and a lower difference between the concentration of recently fallen leaves and mature leaves. This suggests a lower rate of retranslocation in *Swietenia* than *Dacryodes*, a higher quality litter for decomposers and soil organisms, and a greater quantity of nutrient return to the forest floor per gram of leaf litterfall.

The dynamics of nutrient cycling in restored stands will change depending on the species that occupy the site, their abundance, and dominance. A particular species can affect nutrient cycling in different ways depending on the process, its magnitude, timing, and efficiency (Table III). In addition, soil biota plays a significant role in nutrient dynamics and its species composition changes depending on the quality of available litter and soil substrates (Zou and González, 2002).

5. Discussion

From a biogeochemical point of view, restored tropical forests contend with degraded sites where nutrient supply, soil structure, and soil water are not optimal for normal tree regeneration and growth. The level of land degradation limits the capacity of forest stands to acquire nutrients and accumulate biomass. When land degradation is extreme, tree planting is necessary and selection of species, and even fertilization and watering, are needed because tree species differ in their water- and nutrient-use efficiency, and in their capacity for fostering other species (Lugo *et al*., 1990a, b; Wang *et al*., 1991; Parrotta, 1995; Cuevas and Lugo, 1998; Montagnini, 2001, 2002). In addition, the success of tree establishment depends on the ability to concentrate nutrients and water from the soil. Nepstad *et al*. (2001) showed that roots of secondary forest species in the Amazon had the capacity of reaching up to 8 m into the soil profile within 10 to 15 yr of establishment on high bulk density soils. They also had a higher rate of mycorhizal infestations than species of mature forests. The outcome was that within this short time, these secondary forest species were able to restore normal functioning in terms of nutrient and water uptake and recycling.

Once a forest is established, it appears that restored forests attain high ratios of organic matter production to biomass (Figure 2) and their nutrient accumulation and cycling rates (Figure 3) reach levels similar to those of native forests. However, restored forests are young in relation to primary forests and lag mature forests in structural complexity, including coarse woody debris, habitat diversity, biomass (Figure 1), nutrient pools (Table I), and species richness.

Rates of organic matter production and nutrient accumulation are high early in the life of a forest stand and decrease with age or time since disturbance (Figures 1a and 3). The first decade of forest establishment is a time of rapid exchange of organic matter and nutrients between vegetation and soil. Such high rates of exchange influence soil fertility and soil organic matter (Reddy, 2002), as was demonstrated by Silver *et al*. (2000) in a literature review and by Silver *et al*. (in press) at La Condesa. In that forest (Table IV), it took several decades for trees to reverse the soil carbon balance from a source to a sink, and allow a significant acceleration of aboveground primary productivity.

The measured changes at La Condesa were associated with a change in tree species composition from the 13 initially planted on 1937 to 75 species at age 55. It is apparent that species composition is an important aspect of the establishment and functioning of restored forests. Part of the reason is that under degraded conditions the initial pool of species available for colonization is small and usually alien. Restorationists have opportunities to match species to sites, particularly when site conditions are extreme. Because species differ in the acquisition, retranslocation, and nutrient return capacity, they can either accelerate nutrient cycling or slow it down. As species richness increases, natural forces and self-organization come into play and it is not practical to control the species composition of restored sites.

TABLE IV

Characterization of a 55 yr-old subtropical moist forest restored through planting of 13 tree species on a degraded pasture at La Condesa, Luquillo Experimental Forest, Puerto Rico. Data are from Silver *et al*. (in press). Data are based on trees >9.1 cm in diameter at breast height and a forest area of 4.64 ha

Parameter	Value
State variable (Mg ha^{-1})	
Soil organic matter	204
Aboveground biomass	160
Root biomass	2.5
Annual rates (Mg ha^{-1})	
Accumulation of tree species	1 species a^{-1}
Accumulation of aboveground biomass	2.8
Litterfall	10.6 to 12.9
Aboveground net primary productivity	14.9
Root productivity	0.3
Net primary productivity	15.4
Soil organic matter accumulation	1.8
Net soil organic matter sink	1.1

As a result, nutrient and biomass dynamics approach those of natural forests. The time required to attain high rates of primary productivity and nutrient cycling takes decades and depends on the severity of the original land degradation.

Acknowledgements

This study is in collaboration with the University of Puerto Rico (UPR). It is part of the USDA Forest Service contribution to the National Science Foundation Long-Term Ecological Research Program at the Luquillo Experimental Forest (Grant BSR-8811902 to the Institute for Tropical Ecosystem Studies of the UPR and the International Institute of Tropical Forestry, USDA Forest Service). We thank G. Reyes and M. Alayón for their help in the production of the manuscript and J. Morales, T. Hueth, and F. Scatena for their review of the manuscript.

References

Aide, T. M., Zimmerman, J. K., Herrera, L., Rosario, M. and Serrano, M.: 1995, 'Forest recovery in abandoned tropical pastures in Puerto Rico', *For. Ecol. Manage.* **77**, 77–86.

Ashton, M. S., Gunatilleke, C. V. S., Singhakumara, B. M. P. and Gunatilleke, I. A. U. N.: 2001, 'Restoration pathways for rain forest in southwest Sri Lanka: A review of concepts and models', *For. Ecol. Manage.* **154**, 409–430.

Attiwill, P. M. and Leeper, G. W.: 1987, *Forest Soils and Nutrient Cycles*, Melbourne University Press, Australia, pp. 202.

Bernhard-Reversat, F. and Loumeto, J. J.: 2002, 'The litter system in African forest-tree plantations', in V. M. Reddy (ed.), *Management of Tropical Plantation-forests and Their Soil-litter System*, Science Publishers Inc., Enfield, New Hampshire, U.S.A., pp. 11–39.

Bowen, G. D. and Nambiar, E. K. S.: 1984, *Nutrition in Plantation Forests*, Academic Press, New York, New York, U.S.A., pp. 516.

Brown, S. and Lugo, A. E.: 1982, 'The storage and production of organic matter in tropical forests and their role in the global carbon cycle', *Biotropica* **14**, 161–187.

Brown, S. and Lugo, A. E.: 1990, 'Tropical secondary forests', *J. Trop. Ecol.* **6**, 1–32.

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

Brown, S. and Lugo, A. E.: 1994, 'Rehabilitation of tropical lands: A key to sustaining development', *Restor. Ecol.* **2**, 97–111.

Cuevas, E. and Lugo, A. E.: 1998, 'Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species', *For. Ecol. Manage.* **112**, 263–279.

Edwards, P. J.: 1982, 'Studies of mineral cycling in a montane rain forest in New Guinea, V, Rates of cycling in throughfall and litter fall', *J. Ecol.* **70**, 807–827.

Edwards, P. J. and Grubb, P. J.: 1982, 'Studies of mineral cycling in a montane rain forest in New Guinea, IV, Soil characteristics and the division of mineral elements between the vegetation and soil', *J. Ecol*. **70**, 649–666.

Field, C. D. (ed.): 1996, *La Restauración de Ecosistemas de Manglar*, Sociedad Internacional Para Ecosistemas de Manglar, College of Agriculture, University of Ryukyus, Okinawa, Japan, pp. 278.

Food and Agriculture Organization: 1993, 'Forest resources assessment 1990, Tropical countries', FAO Forest Paper 112, Rome, Italy, 61 pp. + appendices.

Food and Agriculture Organization: 2001a, 'Rehabilitation of degraded sites', *Unasylva* **52**, 1–60.

Food and Agriculture Organization: 2001b, 'State of the World's Forests 2001', Rome, Italy, pp. 181.

Francis, J. K.: 1989, 'The Luquillo Experimental Forest Arboretum', Res. Note SO-358, Southern Forest Experiment Station, USDA Forest Service, New Orleans, Louisiana, pp. 8.

Frangi, J. L. and Lugo, A. E.: 1985, 'Ecosystem dynamics of a subtropical floodplain forest', *Ecol. Monogr.* **55**, 351–369.

Holdridge, L. R.: 1967, *Life Zone Ecology*, Tropical Science Center, San José, Costa Rica.

Lugo, A. E.: 1992, 'Comparison of tropical tree plantations with secondary forests of similar age', *Ecol. Monogr.* **62**, 1–41.

Lugo, A. E., Wang, D. and Bormann, F. H.: 1990a, 'A comparative analysis of biomass production in five tropical tree species', *For. Ecol. Manage.* **31**, 153–166.

Lugo, A. E., Cuevas, E. and Sánchez, M. J.: 1990b, 'Nutrients and mass in litter and top soil of ten tropical tree plantations', *Plant Soil* **125**, 263–280.

Lugo, A. E. and Murphy, P. G.: 1986, 'Nutrient dynamics of a Puerto Rican subtropical dry forest', *J. Trop. Ecol.* **2**, 55–76.

Lugo, A. E. and Fu, S.: 2002, 'Structure and dynamics of mahogany plantations in Puerto Rico', in A. E. Lugo, J. Figueroa Colón and M. Alayón (eds), *Big-leaf Mahogany: Genetics, Ecology, and Management*, Springer-Verlag, New York, New York, U.S.A., pp. 288–328.

Medina, E. and Cuevas, E.: 2002, 'Comparative analysis of the nutritional status of mahogany plantations in Puerto Rico', in A. E. Lugo, J. Figueroa Colón and M. Alayón (eds), *Big-leaf Mahogany: Genetics, Ecology, and Management*, Springer-Verlag, New York, New York, U.S.A., pp. 129–145.

Molina Colón, S.: 1998, 'Long-term recovery of a Caribbean dry forest after abandonment of different land uses in Guánica, Puerto Rico', *Ph.D. Thesis*, University of Puerto Rico at Río Piedras, Puerto Rico, pp. 271.

Montagnini, F.: 2001, 'Nutrient considerations in the use of silviculture for land development and rehabilitation in the Amazon', in M. E. McClain, R. L. Victoria and J. E. Richey (eds), *The Biogeochemistry of the Amazon Basin*, Oxford University Press, England, pp. 106–121.

Montagnini, F.: 2002, 'Tropical plantations with native trees: Their function in ecosystem restoration', in V. M. Reddy (ed.), *Management of Tropical Plantation-Forests and their Soil-litter System*, Science Publishers Inc, Enfield, New Hampshire, U.S.A., pp. 73–94.

Nepstad, D., Moutinho, P. R. S. and Markewitz, D.: 2001, 'The recovery of biomass, nutrient stocks, and deep soil functions in secondary forests', in M. E. McClain, R. L. Victoria and J. E. Richey (eds), *The Biogeochemistry of the Amazon Basin*, Oxford University Press, England, pp. 139–155.

Parrotta, J. A.: 1995, 'Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site', *J. Veg. Sci.* **6**, 627–636.

Parrotta, J. A. and Turnbull, J. W. (eds): 1997, 'Catalyzing native forest regeneration on degraded tropical lands', *For. Ecol. Manage*. **99**, 1–290.

Reddy, V. M. (ed.): 2002, *Management of Tropical Plantation-Forests and their Soil-litter System*, Science Publishers Inc., Enfield, New Hampshire, U.S.A., pp. 422.

Saldarriaga, J. G.: 1994, 'Recuperación de la selva de "Tierra Firme" en el alto río Negro Amazonia colombiana-venezolana', *Estudios en la Amazonia Colombiana* **5**, 1–201, Editorial Presencia, Colombia.

Sánchez, M. J., López, E. and Lugo, A. E.: 1997, 'Chemical and physical analyses of selected plants and soils from Puerto Rico (1981–1990)', USDA Forest Service, International Institute of Tropical Forestry, *Research Note IITF-RN-1*, pp. 112.

Silver, W. L., Ostertag, R. and Lugo, A. E.: 2000, 'The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands', *Restor. Ecol.* **8**, 394–407.

Silver, W. L., Kueppers, L. M., Lugo, A. E., Ostertag, R. and Matzek, V.: 'Carbon sequestration and plant community dynamics following reforestation of tropical pasture', *Ecological Applications* (in press).

Toh, I., Gillespie, M. and Lamb, D.: 1999 'The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site', *Restor. Ecol.* **7**, 288–297.

Wang, D., Bormann, F. H., Lugo, A. E. and Bowden, R. D.: 1991, 'Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa', *For. Ecol. Manage.* **46**, 1–21.

Zou, X. and González, G.: 2002, 'Earthworms in tropical tree-plantations: Effects of management and relations with soil carbon and nutrient use efficiency', in V. M. Reddy (ed.), *Management of Tropical Plantation-forests and their Soil-litter System*, Science Publishers Inc., Enfield, New Hampshire, U.S.A., pp. 289–301.