Chapter 19
Research in the Luquillo Experimental Forest Has Advanced Understanding of Tropical Forests and Resolved Management Issues

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Abstract Long-term research on the response of wet forests in the Luquillo Experimental Forest (LEF) to natural and anthropogenic disturbances yielded information useful for the management of these forests and to a better understanding of the functioning of tropical forests and how species composition changes under different disturbance regimes. We summarize studies on basal area removal, response to ionizing radiation, and the effects of hurricanes and landslides on forested watersheds. We also review studies on forested stream biota following hurricane, drought, and flooding events. This chapter also evaluates reforestation of degraded lands and recovery of forests after abandonment of paved roads. All the studies combined cover the major land cover changes that take place throughout the tropics and which require attention to conserve tropical biodiversity. These changes range from limited extractions of resources from forests to deforestation and conversion to pastures. When tropical forests are converted to pastures, more intensive management actions are needed to restore lands, including planting of introduced species capable of growing on degraded lands. Results from the LEF have demonstrated the high resistance and resilience of tropical forests and the success of plantings in the restoration of forest cover on degraded lands. In both streams and forests, species composition shifts from native to introduced species when anthropogenic disturbance regimes become prevalent over the natural disturbance regimes.

Keywords Disturbance · Management · Recovery · Resilience · Succession · Anthropogenic · Species · Streams · Tropical

19.1 Introduction

Tropical watersheds are subject to many types of human modification ranging from removal of individual organisms to deforestation and stream channel modification. These systems are also subjected to a wide range of natural disturbances that in

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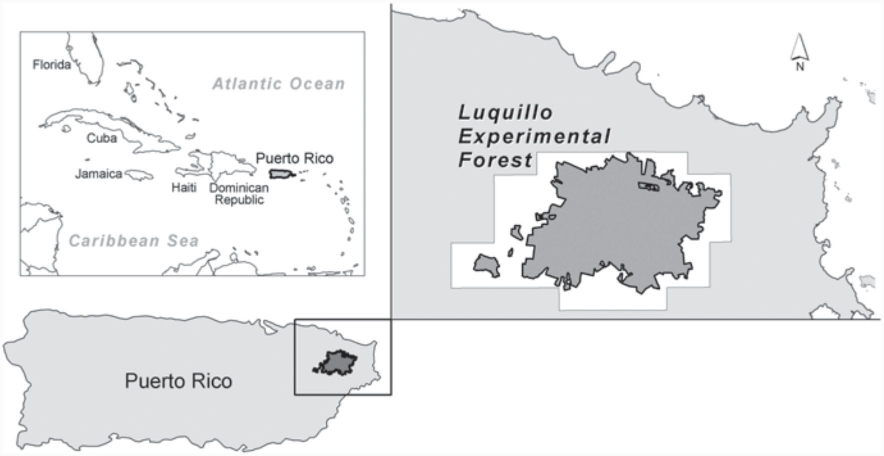

Fig. 19.1 The Luquillo Experimental Forest in northeast Puerto Rico

the Caribbean include hurricanes, landslides, floods, and drought. The net result of the synergy between anthropogenic activity and natural disturbances is a landscape with a mosaic of land covers that range from bare lands to mature forest stands, and ecosystems in different stages of succession following different types of disturbance events. The high density of species that characterize tropical ecosystems and the poor scientific understanding of tropical forest watersheds exacerbate managing this complexity of land covers and ecosystem states.

In this chapter, we review the results of studies on disturbance of ecology that led to better understanding of tropical forest watersheds in the wet Caribbean and to their management and restoration. Specifically, we focus on research that manipulated forest basal area; exposed forest stands to ionizing radiation; experimented with tree cutting and reforestation with introduced species; and studied hurricane, landslide, drought, and flood effects on forests and streams. After summarizing the research, we discuss the societal implications of the research and how these studies have led to long-term research programs and networking with other research sites.

Our main focus is on the Luquillo Experimental Forest (LEF) located in the Luquillo Mountains in eastern Puerto Rico (Fig. 19.1). Within the LEF, we review mostly research in watersheds within the subtropical wet forest life zone (*sensu* Holdridge 1967) and forest stands dominated by *Dacryodes excelsa,* known as tabonuco forest. However, where appropriate, we present research from the subtropical moist forest at lower elevation from the tabonuco forest or forests above the cloud condensation point, which occurs at 600 m in the LEF. Tabonuco forests occur from about 200 to about 600 m elevation.

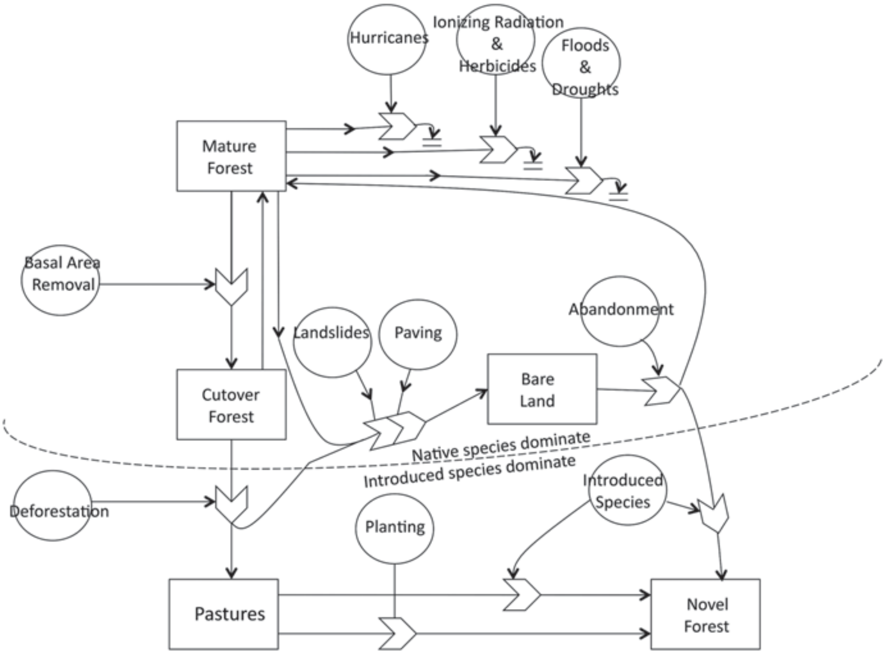

Fig. 19.2 Diagram of land cover change and successional pathways of forests in relation to anthropogenic and natural disturbances in the Luquillo Mountains of Puerto Rico. *Circles* represent external forces that cause change in the land cover and biota. The text contains a discussion of each of these disturbances or human actions. *Boxes* represent a land cover including forested, pastures, or bare lands. The *large arrow* symbol illustrates the interaction between an action or disturbance and a flux or change in land cover or forest state. For hurricanes, ionizing radiation, herbicides, floods, and droughts, the effect is a stress on the system and does not involve a change in cover or successional pathway. *Lines with arrows* illustrate the successional pathways and their direction. Native species dominate those states *above the dotted line,* and introduced species dominate those *below the dotted line.* This system is driven by climate and solar energy, but those forces are not shown. The text contains more discussion of this diagram

19.2 Land Cover Changes and Disturbances in the Study Area

To place the studies that we review in context, we developed a heuristic diagram of land cover change and disturbance effects in the Luquillo Mountains (Fig. 19.2). The diagram shows three distinct land covers (forested, bare land, and pastures), three forest states (mature, cutover, and novel), four natural disturbances (hurricanes, floods, drought, and landslides), three experimental disturbances (removal of basal area, ionizing radiation, and planting), two anthropogenic interventions (deforestation and land abandonment), and a variety of successional pathways and responses to disturbances powered by sunlight (not shown).

Land covers change from forested to pasture or bare land depending on the intensity of the anthropogenic or natural disturbance, but all land covers can be reversed towards forest maturity through natural succession or through intervention by planting. Species composition can change if plantings involve introduced species or if conditions through succession favor introduced species. Understanding these changes has been one of the main objectives of long-term research in the LEF.

The processes of land cover and ecosystem state changes and responses to disturbances depicted on Fig. 19.2, with the exception of the experimental treatments, occur in most tropical landscapes within the hurricane belt. Outside the hurricane belt, other natural disturbances such as fires become predominant. Within the Luquillo Mountains, the Forest Service faced a management challenge when it tried to restore deforested lands with temperate zone-based approaches (Wadsworth 1995). Research was needed to develop land rehabilitation strategies, particularly species selection, and to understand the importance of biodiversity to ecological functions. The results of the studies that follow, although conducted independently over a period of about 60 years, provide insights into the management of complex tropical landscapes by shedding light into the response of tropical forests and streams to both anthropogenic and natural disturbances in terms of changes in structure, species composition, and rates of ecological processes.

19.3 Hurricanes and Other Stressors Shape Forest Structure and Functioning

Schimper (1903), one of the early ecophysiologists to write about tropical rain forests, noted the importance of abundant rainfall to the delimitation of rain forests. However, while abundant rainfall is vital for sustaining forest growth and its quantity correlates with species richness and epiphyte abundance (Gentry 1982), when a forest is exposed to too much rainfall, water becomes a stress to plants and adaptations are required for their survival. This stress is true in parts of the LEF, where research has revealed a long list of plant attributes for coping with high rainfall (Table 19.1). In general, forest complexity measured as the product of basal area, tree density, maximum tree height, number of tree species, and the constant 10^3 (all expressed per 0.1 ha), increases with rainfall (Holdridge 1967). Paradoxically, the wettest elfin forests in the LEF are shorter and have lower rates of primary productivity than tabonuco forests that receive less rainfall (Weaver and Murphy 1990).

While rainfall can influence the physiological behavior of plants and animals at the LEF (Lugo 1986; Lugo and Scatena 1995), it is the influence of wind that appears to be the dominant factor in the shaping of forest structure and tree species density (Lugo 2008). After Hurricane Hugo affected the Caribbean in 1989, Brokaw et al. (2004) found support for the role of hurricanes in shaping forest canopy

Table 19.1 Effects of water on, and forest response to, too much water in wet and rain forests. (Lugo 1986)

Effects
Tree growth, seed germination, explosive seedling growth, leaf fall, flowering, and fruiting are all synchronized to slight changes in rainfall, which was documented in the Luquillo Experimental Forest
Bromeliads and other epiphytic organisms store water within their leaves, and large and diverse populations of animals utilize these as habitats and for reproduction
Tap roots, abundance of deciduous species, and tree growth rings, which are normal responses to moisture seasonality, are not usual features in the forests of the Luquillo Experimental Forest
Response to too much water
Epiphytic coverage of surfaces increases with increasing moisture, which in turn, contributes to an even distribution of throughfall by temporarily storing water and reducing its impact on other surfaces
Epiphytes also absorb nutrients from incoming waters and this contributes to a reduction in the loss of minerals to downstream ecosystems
Anatomical and morphological characteristics of plants at high elevations and low saturation deficits contribute to the increase in transpiration rates. For example, number and size of stomata increase with altitude
Where saturation deficits are high, anatomical and morphological characteristics of plants reduce water loss
Palms develop massive adventitious roots laden with lenticels that contribute to root gas exchange in anaerobic soils
Surface and adventitious roots increase dramatically with increasing water logging of soils
Trees maintain epiphyte-laden old leaves for long time periods in spite of the low Photosynthesis over respiration ratio of these leaves. It appears that their role in mineral cycling and nutrient conservation has more selective advantages than their role as net organic matter producers
Forests have extensive root mats that are essentially mineral-tight
Plants flower for longer periods in the wetter sites and depend on insects and birds for pollination

structure. In Puerto Rico, the LEF has the richest flora in the island because the mountain gradient encompasses an annual rainfall range from about 2,000 to more than 5,000 mm. Nevertheless, at the scale of a hectare, all island forests, regardless of rainfall, have a similar tree species density of about 60–70 species (Lugo 2005). This is in spite of an insular rainfall gradient from about 800 to more than 5,000 mm. The similarity in species density is not an insular effect because similar observations have been made elsewhere (insular or continental) where hurricanes are the dominant natural disturbance (Lugo 2008). The point to be made is that hurricane winds, persistent trade winds, and high rainfall are physical factors that strongly influence the biota in terms of its species composition, community structure, and ecosystem functioning. These are the primary natural factors to be considered when interpreting long-term phenomena in Caribbean forests. As we will see below, anthropogenic factors also exert strong influences on forests and they require consideration, particularly outside the LEF. The LEF is an insular standard for the maturity of its vegetation and the reduced effects of anthropogenic disturbances on its ecosystems.

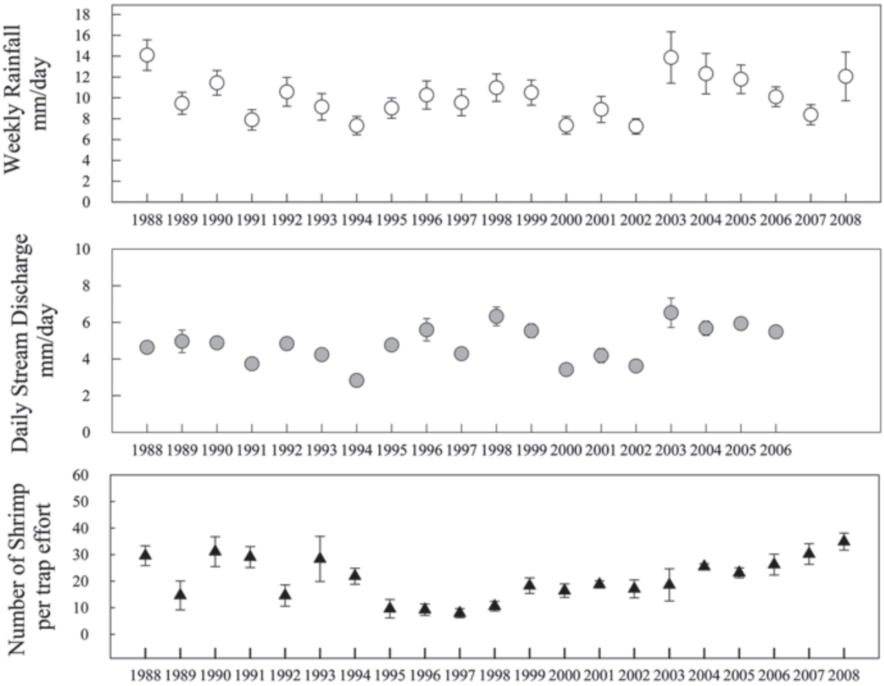

Fig. 19.3 Mean weekly rainfall and daily stream discharge in the Bisley Experimental Watersheds, and number of shrimp per trapping effort in Prieta Stream, Luquillo Experimental Forest, Puerto Rico. (Data sets are available at http://luq.lternet.edu/data/luqdata)

19.4 Droughts and Floods Have Greater Short-Term Effects on Shrimp Populations than Hurricanes

Stream ecosystems in the LEF are tightly coupled with the environmental conditions of their surrounding forest landscape. Even though there is relatively high mean daily rainfall in the LEF (Heartsill Scalley et al. 2007), there is relatively little water storage capacity in the river systems, which have high gradient streams that drain into the ocean within a very short distance traveled to the coastal plain. There is a tight link between rainfall, headwater stream discharges, and shrimp abundances in these streams (Fig. 19.3). Both rainfall events with record-breaking intensity and prolonged drought periods have been observed in the LEF (Table 19.2). These decreased rainfall events affect the stream environment by dramatically decreasing water flow levels, pool depths, and altering stream substrata. Consequently, these drought effects alter short-term shrimp population dynamics more than past hurricane events (Covich et al. 2006; Table 19.3). Extremely low flows persist during prolonged drought and reduce physical habitat availability for stream fauna, as well as affect other aspects such as migration, dispersal, and flow-related fauna communication among prey and their predators (Crowl and Covich 1994; Covich

Table 19.2 Weeks with extreme rainfall events in the past 20 years, 1988–2008 in the Luquillo Experimental Forest, Puerto Rico

Number of weeks				
Year	>40 mm/d	50–60 mm/d	>60 mm/d	Local drought
1988	1	0	0	1
1989	0	0	0	3
1990	0	0	0	0
1991	1	0	0	1
1992	0	1	0	3
1993	0	1	0	2
1994	0	0	0	3
1995	0	0	0	4
1996	1	1	0	3
1997	1	0	0	5
1998	2	0	0	3
1999	0	0	0	3
2000	0	0	0	2
2001	1	0	0	7
2002	0	0	0	2
2003	0	0	2	2
2004	2	0	1	2
2005	1	0	0	2
2006	0	0	0	1
2007	0	0	0	3
2008	2	0	2	0
Total	*12*	*3*	*5*	*52*

Local drought events are defined as 5 % of the times in the 20-year record with low or no throughfall, equivalent to 0.5 mm per day (mm/d)

et al. 2003). Stream channel structure and heterogeneity are altered during droughts, as riffles become constrained and dry out, causing pools to become disconnected, which in turn leads to a decrease in downstream dispersal of larvae; upstream migration of postlarvae; and downstream flow of leaves, branches, wood, and other organic matter. Organic matter accumulation and low or no flow downstream reduce pool volume and can further alter the quality of the physical habitat by decreasing dissolved oxygen. From the perspective of the stream physical habitat, hurricanes can produce a combination of cumulative effects that are also produced by other disturbances. For example, some are similar to those that occur during droughts, as pools can become disconnected due to debris dams and organic matter accumulation, while other effects are similar to those of floods, such as washout and scouring. The aquatic fauna of these streams have life history strategies that can sustain their populations following the change in physical conditions after the passing of hurricanes, and their populations have been observed to recover rapidly after such events (Covich et al. 1991). However, the cumulative effects of more frequent and intense hurricanes, coupled with more drought effects, could greatly alter these populations. Moreover, anthropogenic activities such as harvesting of larger species for human

Table 19.3 Observed effects of droughts, floods, and hurricanes on shrimp stream habitat in the Luquillo Experimental Forest, Puerto Rico

←Less resilience		More resilience→
Drought	Flood	Hurricane
Habitat loss: riffles dry out, shallow headwater pools disappear, and stream channels narrow	Temporary habitat loss: high water flows wash out individuals from headwater reaches	High water flows occur and debris dams are formed throughout the stream elevation gradient
Physical habitat fragmentation	Scouring and washout of physical habitat	Debris dams decrease washout of individuals
	Temporary habitat loss: high overland water flows can increase landslides and increase silt levels enough to decrease quality of habitat in headwater reaches	Debris dams retain water and organic matter
	Access to quality habitat and food sources decreased (silted surfaces affect periphyton and algal growth)	Debris dams slowly release water and organic matter during following months
Increased predation: lower pool water levels and fragmentation increases encounters with predators	Increased predation in new temporary habitat (lower elevation pools)	
Decrease of water oxygen levels from lack of stream flow		Retained particles are slowly released, an alternate food source to particulates of green and brown litter fall at various stages of decomposition
Loss of dissolved organic matter from lack of stream flow and habitat fragmentation		Movement towards headwater reaches from mid-elevation sites
Possible increase in anoxic conditions in decreased and fragmented pool riffle habitat		Restructuring of stream pools and riffles, but no net loss or fragmentation occurs

We use temporary habitat loss because immediate upstream migration can occur

consumption and dam construction can diminish populations when combined with increased natural disturbances such as more frequent hurricanes and droughts.

Most of the tropical island stream fauna in the LEF, including fish, shrimp, and snails, have to migrate between the stream freshwater habitats to the saltwater estuarine and coastal habitats to complete their life cycles. Aquatic insects disperse by flying as adults and freshwater crabs complete their life cycle in headwater streams and do not migrate to coastal waters. The freshwater shrimp that dominate the streams of the LEF spend their lives as adults in the headwater streams and rivers where they feed, grow slowly, and reproduce (Cross et al. 2008). The gravid, egg-carrying, female shrimp then release larvae into the flowing water. Larvae drift with the current downstream all the way to estuarine waters where they will remain in this drifting, planktonic stage until they develop into postlarval juveniles (Covich and McDowell 1996; Benstead et al. 2000; Scatena 2001; March et al. 2003). As post larvae, they migrate upstream where they can occupy pools that serve as spatial refugia from fish predators once they climb steep waterfalls that are barriers to predatory fishes (Covich et al. 2009; Kikkert et al. 2009). This migratory life cycle is classified as amphidromous, and it is also observed in other native aquatic species such as gobiid fishes and neritina snails (March et al. 2003; Blanco and Scatena 2006; Covich 2006).

During a 15-year span that included two hurricane events (Hurricane Hugo in 1989 and Georges in 1998) and one prolonged, island-wide drought in 1994, Covich et al. (2006) measured shrimp abundances along the elevation gradient of Quebrada Prieta, a stream that flows into the Espiritu Santo, one of the major rivers of the LEF. They found that hurricanes and storm flows had no persistent measurable effect on pre- and post-event shrimp abundances when compared with the drought, which decreased shrimp abundance in headwater streams. During low flows, there was a loss of chemical cues (Crowl and Covich 1994) and increased predation (Covich et al. 1996). Droughts primarily alter physical habitat and spatial refugia from predatory fishes and these changes affect populations of aquatic species over several years. In contrast, flood events have different effects on particular species and these effects relatively short term.

Flood events displace more of the shredder than the filter feeder shrimp guilds. Increased vulnerability to washout during high-flow events of shredders is related to their behavior, as the primary species of shredders swim into in the upper open pool areas compared to the main filter feeder species which stay close to the bottom of pools and among crevices in the stream banks and between boulders. However, during extreme flooding events when stream substrata are scoured, both of these guilds can be displaced from the higher-elevation stream reaches to the mid- and lower-elevation stream sections where deeper pools and crevices in the banks can serve as refugia (Covich et al. 1996).

Following high-wind events, leaves and woody branches removed from riparian trees form organic debris dams. During prolonged droughts, these dams can contribute to loss of connectivity among pools and lower water quality by decreasing available oxygen levels in pools with accumulated and decomposing organic matter. In general, the organic debris dams ameliorate the effects of high flows during hurricanes and other tropical storms. Hurricanes can produce sustained floods in headwater reaches and drainage-wide high-flow events, which can be buffered by debris dams resulting from high-wind events. In the wider channels downstream, larger flows tend to wash out debris dams and deposit wood along riverbanks. During hurricane events, dams maintain habitat heterogeneity, which sustain shrimp abundances in headwater streams (Covich et al. 2006).

Stream ecosystems in headwaters are tightly coupled with rainfall and inputs from forested riparian areas that serve as an energy source for aquatic fauna (Crowl et al. 2006). High rainfall and almost no water storage capacity in the river systems means that the role of riparian vegetation in providing structure and connectivity is crucial to sustaining the stream ecosystem and the services it provides. Coupled rainfall, stream discharge, and shrimp abundance (Fig. 19.3) indicate that watershed management needs to consider the intrinsic forest and stream connections, which means not disrupting the migration of native fauna and minimizing the alteration of riparian and wetland zone vegetation. In one of the main rivers whose headwaters are in the LEF, the Mameyes River, an innovation in water resources management allows water flow to remain unobstructed while it is able to provide water for local consumption. Backed by research that spans over two decades, the river contains a unique water extraction system. This low-impact system allows for continuous fauna migrations without interrupting water flow and stream ecosystem connectivity as low-head dam barriers do. This within-channel withdrawal system is located near the center of the channel nestled within its substrate and away from the bulk of the water flow (Scatena 2001; March et al. 2003). The placement of this system resulted in minimum river channel and upstream habitat modification, in addition to a lack of interruption of larval migration and unobstructed base flow levels that also address local water consumption needs.

19.5 Basal Area Reduction Experiments and Monitoring Uncover Controls of Tree Growth

Since 1943, 420 plots of 0.1 ha were established in the tabonuco forest of the LEF to monitor tree growth in support of the preparation of a land management plan and to study tree growth in complex tropical forests. These plots were dispersed on the landscape ranging in elevation from 200 to 640 m. Thousands of trees with diameter at breast height (dbh) > 9.1 cm were identified to species, tagged, and measured. Plots were remeasured in 1947, 1952, 1958, 1965, 1976, and 1982. Additional tree growth plots were established in other mature forest stands including tabonuco stands. In some of these plots, 50 % of the basal area was experimentally removed to ascertain growth responses. These additional plots were also remeasured periodically over the next several decades.

Reduction of basal area led to increased growth of remaining trees (Fig. 19.4). Closer analysis of growth data revealed the importance of canopy position to tree growth. Trees with dominant canopies (all canopy exposed to light) had the faster growth followed by those with codominant canopies (canopy receives light from the top), intermediate canopies (canopy below the main canopy), and suppressed trees whose canopy is shaded most of the time. In one species, the growth of trees with dominant canopies was four times higher than the growth of trees with suppressed canopies (Parresol 1995). Tree growth also varied with species and topographic position (ridge, slope, and valley), with some species doing better in one or another position (Parresol 1995). Moreover, Wadsworth et al. (2010) identified crop trees from the data set and was able to identify which trees were growing at rates twice as fast as the mean and the conditions associated with the fast growth of these crop trees.

Tree growth information and knowledge of what factors influenced growth rates were used by Wadsworth to develop a scheme for liberating crop trees from

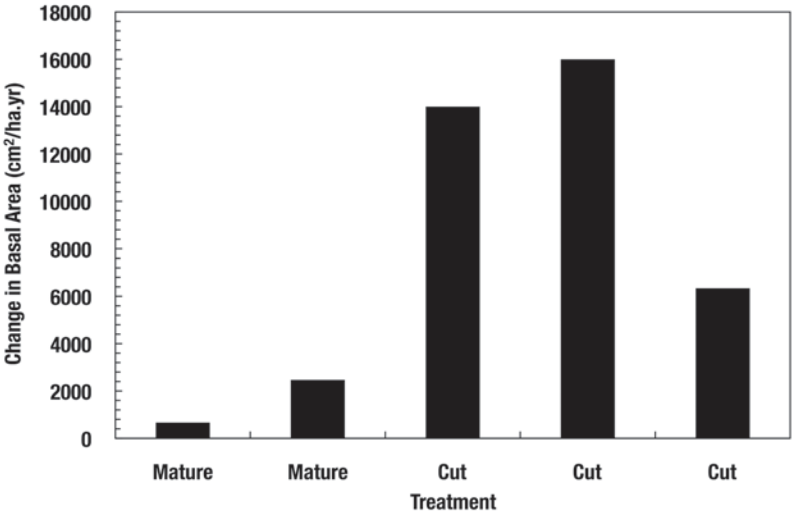

Fig. 19.4 Basal area increase of trees in mature tabonuco forests when compared with trees in tabonuco forests with 50 % basal area reduction (cut). (Data are summarized in Brown et al. 1983)

competition, thus achieving the maximum growth possible (Wodsworth 1997). This scheme was successfully tested in Puerto Rico and exported to Brazil (Wadsworth and Zweede 2006) and Costa Rica (Hutchinson and Wadsworth 2006). In Brazil, the system proved economically feasible as the increased productivity of wood could pay the entire cost of the liberation. Also, increased growth rate reduced by 25 % the time in the wait for the next harvest.

19.6 Ionizing Radiation and Other Disturbances Uncover the Resilience of Tropical Forests

In January 19, 1965, about 2 ha of the LEF was irradiated for 92.8 days with a 10,000-curie cesium (Cs^{137}) ionizing radiation source (Odum and Drewry 1970). The impetus for the study was to learn about how tropical forests might respond to ionizing radiation, should nuclear devices be used to excavate a second Panama Canal between the Pacific and Atlantic Oceans. The study area, which formed a canopy gap as a result of tree mortality, was studied for 23 years (Taylor et al. 1995).

The level of ionizing radiation applied to the tabonuco forest in the LEF was high and initially the forest exhibited a high resistance both at the tree population and forest level. For example, Odum et al. (1970a) reported live trees that had received up to 100,000 R (roentgens) and many with normal appearance in spite of being exposed to 12,000 R. For a year, it was difficult to establish a clear zone of tree mortality around the ionizing radiation source. However, with time, the trees within 40 m of the ionizing radiation source all died and a large gap was created (Taylor et al. 1995). Tree growth declined in several species that survived the ionizing radiation,

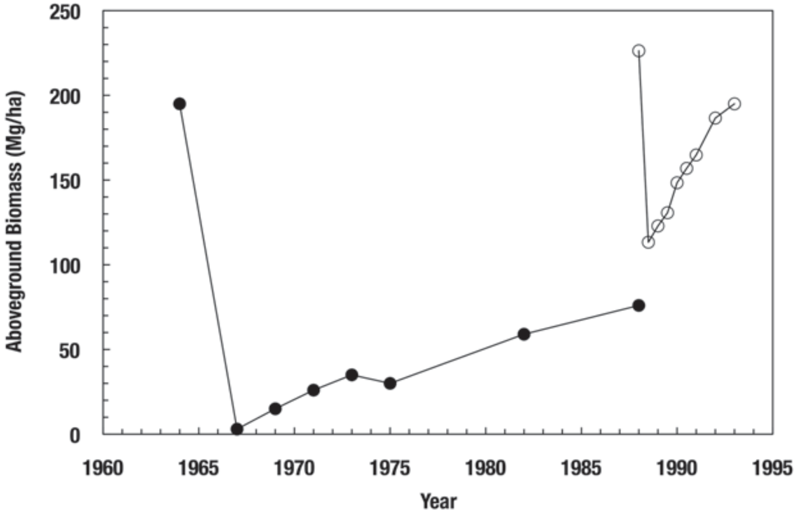

Fig. 19.5 Aboveground biomass after gamma irradiation of a tabonuco forest stand at El Verde (*solid circles*) and after a hurricane passed over a tabonuco forest at Bisley (*open circles*), Luquillo Experimental Forest. Data are from Taylor et al. (1995) and Scatena et al. (1996). The high value in each data set corresponds to the pre-disturbance of aboveground biomass. The reduction after the hurricane was instantaneous while that after irradiation was progressive over several years

but after the event they returned to normal rates of growth, while other species remained at slower rates of growth or increased (Murphy 1970). Successional tree species like *Cecropia schreberiana* accelerated tree growth after ionizing radiation, while primary species like *D. excelsa* reduced growth.

Although many scientists were seeking to document dramatic ionizing radiation effects after the radiation source was shut down, they were mostly unsuccessful in the short term (Odum et al. 1970a). However, long-term data and comparisons of forest response to ionizing radiation with responses to an experimental cut, addition of herbicides, and hurricanes yielded numerous insights on forest resilience and allow us to position ionizing radiation effects in perspective relative to the other disturbances. We focus first on a comparison between ionizing radiation and hurricane disturbance effects on biomass accumulation and productivity, and then compare various disturbances in relation to species composition responses.

Fig. 19.5 shows the aboveground biomass loss and accumulation in two tabonuco forest stands in the LEF, one exposed to ionizing radiation and the other to a category-3 hurricane. The reduction in biomass due to ionizing radiation was much greater than the reduction of biomass due to the hurricane. The hurricane reduced forest stand biomass by 50 %, while ionizing radiation reduced biomass by almost 100 %. This comparison requires some explanation to properly understand how each of the two disturbances affects the forest. The loss of biomass due to ionizing radiation has two caveats. First, the loss, while very high, is limited to a small area receiving high radiation dosages. A meter away from the limit of the mortality zone shows no apparent ionizing radiation effects on trees. Second, the loss of biomass

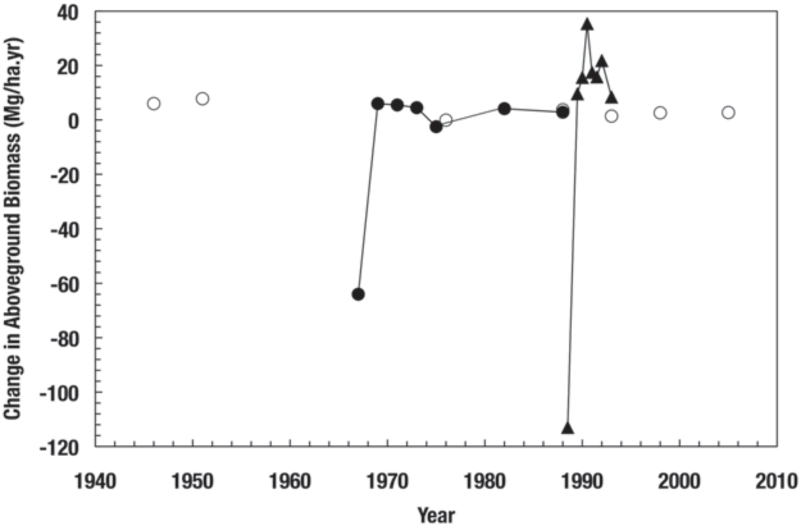

Fig. 19.6 Changes in aboveground biomass of tabonuco forests in different sectors of the Luquillo Experimental Forest. Positive values correspond to growth and negative values to losses to mortality. The long *open circle* data series corresponds to El Verde 3, a mature tabonuco plot (see Lugo et al. in this volume and Drew et al. 2009 for data source and analysis of the behavior of this plot over 62 years). *Solid circles* correspond to the tabonuco plot that was irradiated at El Verde and the *solid triangles* correspond to a tabonuco plot in Bisley (Scatena et al. 1996)

associated with ionizing radiation occurs over a period of years, which is a slow response. Thus, anionizing radiation disturbance delivers a high-intensity effect over a small area (square meters) and over a relatively long time (years). In contrast, the effect of the hurricane disturbance is brief (hours) and over a larger area of landscape (hectares). These different modes of action have contrasting ecological effects in terms of the coupled ecological processes such as wood decomposition, mineral cycling, and carbon dynamics (Lugo and Scatena 1996).

Figure 19.5 also shows that the accumulation of biomass after the disturbance effect follows different slopes for ionizing radiation and hurricanes. This is better illustrated in Fig. 19.6 where rates of loss and accumulation are shown. Biomass accumulation after a hurricane is much faster than biomass accumulation after ionizing radiation. Yet, the rates of biomass accumulation after ionizing radiation are in the same order of magnitude as those measured in a nearby mature tabonuco stand not subject to ionizing radiation. Thus, it appears that the slower recovery of biomass after the ionizing radiation experiment is due mostly to the lower quantity of live biomass that remained after the event reached its peak effects. Of course, the level of residual live biomass was a function of the intensity of the ionizing radiation source. After a hurricane, more live biomass remains standing, and rates of accumulation reach very high values, leading the stand to pre-hurricane biomass in less than 5 years or so for a hurricane such as the one depicted in Fig. 19.7. Another factor that might influence the rate of biomass accumulation is the physiological state of irradiated trees, which could have exhibited reduced photosynthetic capacity as a result of the stress.

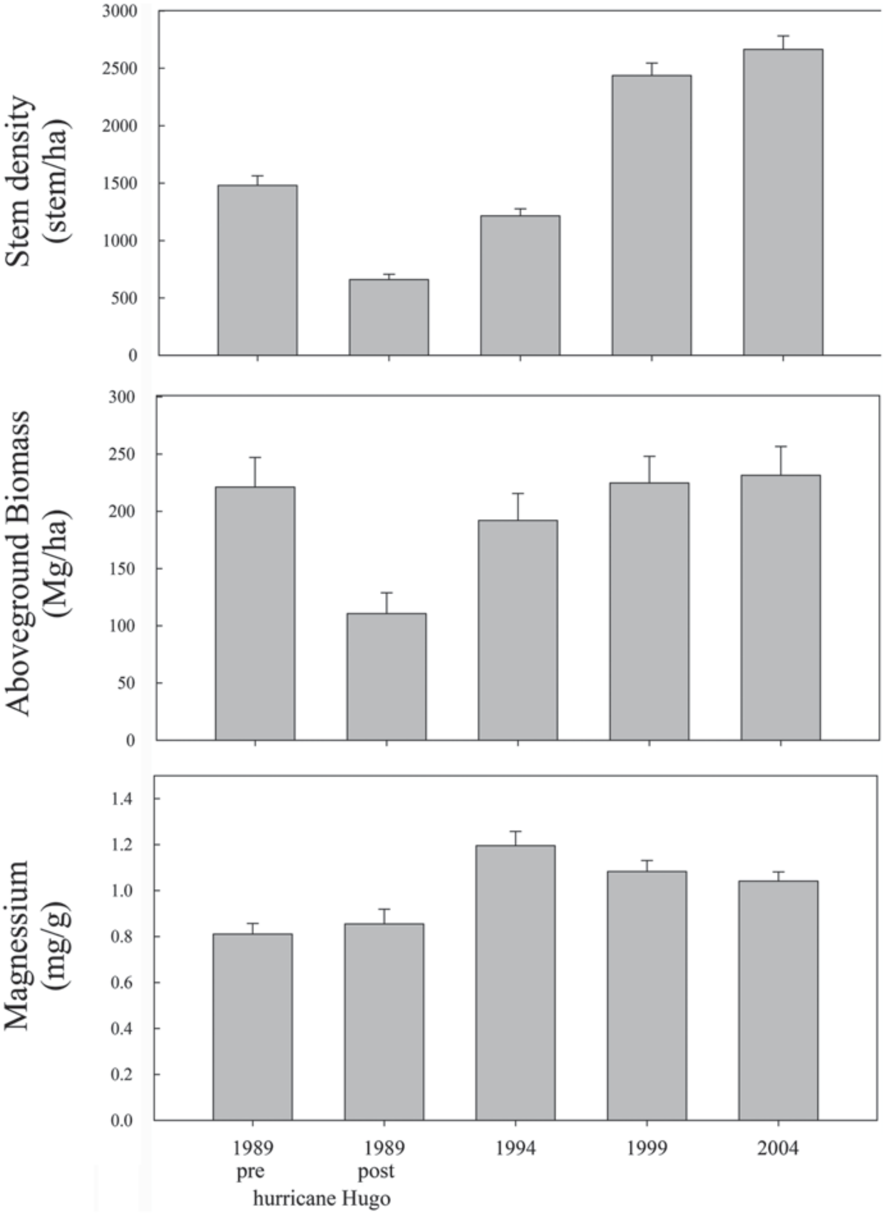

Fig. 19.7 Stem density, aboveground biomass, and magnesium concentration in aboveground biomass in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico

Forest response to disturbances also includes changes in species composition, and at the LEF it has been possible to compare species responses to ionizing radiation, herbicides, hurricanes, and cutting (data, pictures, and discussion in Brown et al. 1983; Odum et al. 1970a; Dowler and Tschirley 1970; Smith 1970). Among the many observations, three stand out from a long-term perspective:

1. In all instances, the regeneration after the disturbances (ionizing radiation, hurricanes, defoliants, or cutting) was composed of native species. Introduced species were not able to regenerate after any of these disturbances.
2. The diversity of plant life-forms increased during regeneration but was particularly notable after irradiation. Normally, the arboreal life-form maintains dominance during regeneration after hurricanes, application of defoliants, and cutting. Seedlings, saplings, and vines dominate the understory. After ionizing radiation, radiation killed most of the original plants including seeds, and the ensuing vegetation was conspicuously herbaceous dominated by graminoids, herbs, vines, root sprouts, ferns, and some palms. These life-forms gave way to seedlings and saplings, but seedlings of primary forest species had not reappeared on the site after 25 years of succession.
3. The disappearance of primary forest species in the succession after irradiation underscores a point about the speed of succession after the various disturbances. Hurricanes and cutting were both followed by vigorous growth of seedlings and saplings, both from the seed and seedling banks of the forest. The same was true of defoliation, although herbicide treatment of soil at high dosages arrested grass regeneration for about a year; the soil was not sterilized for a long period. In terms of initial regeneration, the ranking of disturbed sites in terms of species diversity was highest in cut forest, followed by irradiated forest, and herbicided forest last. Irradiation eliminated the seed and seedling banks and thus the speed of succession was slowed and skewed to those native species capable of reaching and establishing at the site. Even today, 44 years since the ionizing radiation, the species composition at the radiation site has not returned to what it was before, while the cut, herbicided, and hurricane-affected sites recovered relatively quickly, i.e., within 20 years (Heartsill Scalley et al. 2010).

19.7 Forest Recovery from Landslides and Road Abandonment Is Rapid

The ecosystem dynamics of primary succession from bare land in the LEF are rapid, initial biomass accumulation is followed by increasing vegetation cover and finally structure approaches that of forest stands. Consistently, in both landslides and abandoned roads, after 60 years, basal area values are similar to those found in adjacent forests. The observed recovery, or reclaiming of bare land areas by vegetation in the LEF, is also scale dependent because it is affected by the size of the landslide and heterogeneity, as adjacent forest type and its conditions were the most important factors influencing the direction and level of recovery.

Primary succession in the exposed surfaces of landslides and abandoned roads are part of the forest mosaic in the LEF. During a 50-year record (1936–1988), landslides comprised < 1 % of LEF area, while active roads were estimated at close to 0.5 % of the LEF (Guariguata 1990; Karecha 1997). Even though these road and landslide disturbances occupy a small area within of the forest, they are conspicuous features of the landscape, particularly after heavy rains. Landslides and roads are part of the natural and anthropogenic disturbance regime of this forest. Landslides expose weathered rocks and clays in the lower elevations, and saturated silts at the higher elevations of the LEF. Abandoned asphalt roads of a lane and a half width are surrounded by contiguous forest and must first accumulate soils in order to begin any forest recovery processes.

Heyne (2000) found that a strong influence on recovery of soil physical characteristics and nutrients in these abandoned roads was exerted by adjacent forest conditions. This follows the documented high heterogeneity of soils in the LEF, where nutrient pools are influenced by forest dynamics at small spatial scales (Silver et al. 1996). Abandoned paved roads, which ranged in age since abandonment from 4 to 60 years, had litter and soil characteristics similar to their adjacent forest areas after 11 years (Fig. 19.8). Net nitrogen mineralization (grams per gram of dry soil) and percent soil organic matter were not different between abandoned roads and adjacent forest, while soil pH required more than 60 years of abandonment for recovery to forest conditions. Physical accumulation of soil above the pavement was the delaying factor to the full recovery of soil properties. Some sites had litter accumulation levels similar to those observed in the adjacent forest at 11 years of abandonment, but in one site litter recovered after only 4 years (Fig. 19.8). Litter mass on newly deposited soils above roads contributes to changes in environmental conditions by minimizing soil temperatures and providing a physical structure for retaining seeds, creating microhabitat for soil fauna, and minimizing erosive soil loss due to rainfall (Heyne 2000). In contrast, soil characteristics of landslides that were < 1 year old were similar to forest sites only in their bulk density. Landslide soils had lower nutrient concentrations and organic carbon, but similar total phosphorus concentrations to those in forest soils (Guariguata 1990).

Ferns, seedlings, and woody vines dominate understory vegetation developing on abandoned roads (Heyne 2000). Ferns dominate landslides after 30 years of succession following an initial dominance by herbs and grasses, whereas in abandoned roads of similar age, tree densities and number of species reached the same values as those observed in adjacent forests. Canopy structure was similar between abandoned roads and adjacent forests after 40 years of succession. There are different constraints on succession after these two types of disturbances, as seen in how their species composition changes through succession. On landslides, there was an abundance of *C. schreberiana,* a small-seeded, light-demanding pioneer tree species, but this species was not common in the abandoned road sites. Initial differences in species composition result in different successional paths to maturity depending on adjacent forest conditions and scale of disturbance. Small landslides are quickly colonized and progress rapidly towards tree cover because soil disturbance is slight. Larger slides are more heterogeneous and include zones where the soil profile is exported, exposing rock or saprolite and setting succession back to primary suc-

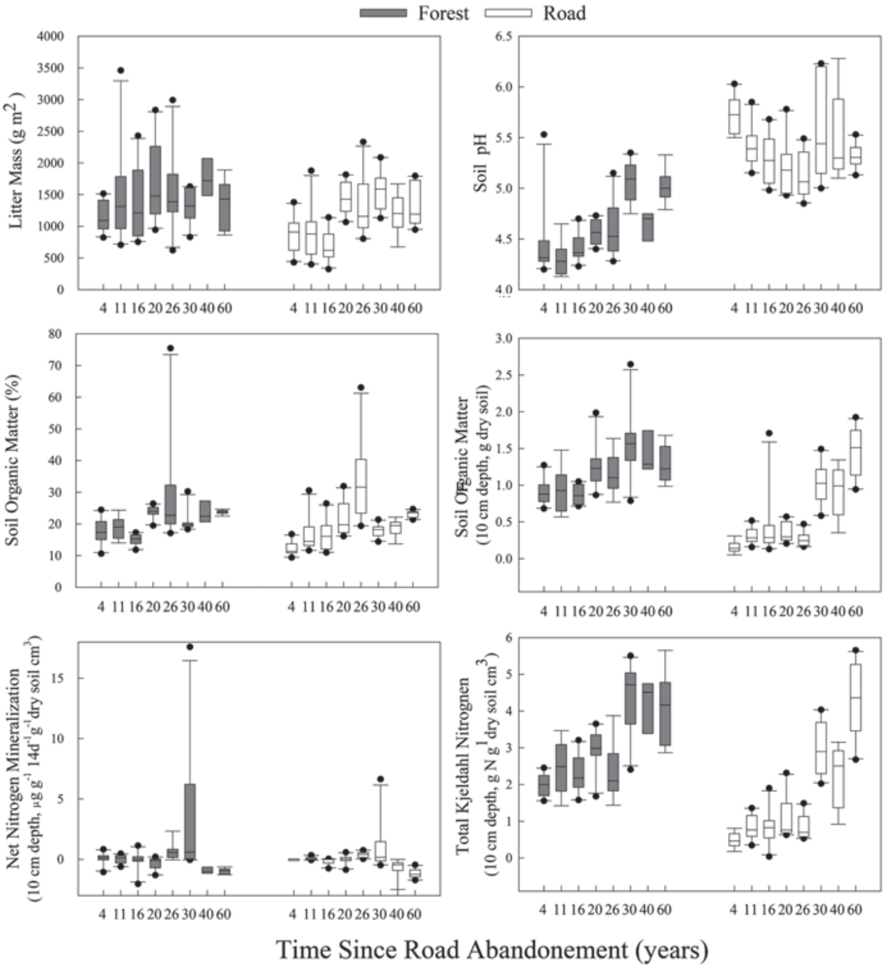

Fig. 19.8 Changes in various soil parameters in chronosequences of abandoned roads and adjacent forests of similar age in the Luquillo Experimental Forest, Puerto Rico. *Boxplots* represent distribution of data points (Heyne 2000), each box encompasses the 25th through 75th percentile, and the *horizontal lines* mark the median and 10th and 90th percentiles

cession. In older landslides and roads abandoned for more than 30 years, the palm *Prestoea montana* reached similar or greater abundances than those in adjacent forest areas (Guariguata 1990; Heyne 2000). However, the vegetation on these newly exposed terrains (landslides, abandoned roads, and roadside filled areas) remained different in species composition from that of nearby forest areas even after 60 years. Floristic composition began to approximate, but did not attain, mature forest species composition at any of the measured sites (Guariguata 1990; Walker et al. 1996; Olander et al. 1998; Heyne 2000).

19.8 Tree Planting on Abandoned Pastures Results in Long-Term Carbon Sinks

A common land management problem in the tropics is overcoming arrested succession on deforested and degraded lands that are invaded by grasses. These grasslands or abandoned pastures are hostile environments for trees, and remain as pastures for decades because tree regeneration without active management does not occur (Parrotta 1999). This problem of land restoration was resolved in the LEF through extensive experimental plantings of native and introduced tree species (Marrero 1950). One such planting involving nine native and four introduced tree species was evaluated for its carbon sequestration outcome 55–61 years after the initial plantation (Silver et al. 2004).

The forest was planted on degraded pasturelands in the subtropical moist forest life zone of Holdridge (1967). Over the next 61 years, it had accumulated 75 tree species or 62 more than were planted, with 60 % of the importance value accounted by native tree species (Table 19.4). The growth of trees was not uniform over the 61-year period as trees increased in basal area faster as the forest matured (Fig. 19.9). The forest rapidly accumulated carbon both aboveground and belowground, with greater carbon storage belowground (Table 19.4). Fine root biomass was in the same order of magnitude as measured in mature native forests (Silver et al. 2004).

Planting trees on degraded pasturelands not only resulted in a species-diverse forest but it also transformed the distribution and accumulation of carbon on the site. Isotope work showed how forest-derived carbon accumulates steadily over the soil profile, while pasture carbon declines (Fig. 19.10). However the increase in forest-derived soil carbon was faster than the decrease, causing a net carbon sink of about 33 Mg/ha over the 61-year period. Moreover, the accumulation of belowground fine root and aboveground biomass, as well as litterfall rates, was all high and contributed to the overall carbon sink of the planted forest (Table 19.4).

19.9 Introduced Species Cannot Dominate Native Forests but Form Novel Forests on Degraded Lands

We noted in the previous section that native species were the only ones regenerating after hurricanes, clearcuts, irradiation, and application of defoliants to tabonuco forests. We also pointed out that the vegetation of the LEF is among the most pristine in Puerto Rico and contains the largest area of primary forest in the island (Lugo 1994). A reason why introduced species have so little success might be the dominance of native species and the undisturbed condition of these closed-canopy forests within the LEF. However, there are many introduced and established populations of plants and animals in this experimental forest. They help explain why the balance between introduced and native species favors the native species.

Along highways and recreation areas where human activity is concentrated, one finds many introduced species, mostly because they were planted or abandoned and fed (in the case of stray dogs and cats). As we will see subsequently, introduced plants,

Table 19.4 Long-term outcomes in ecosystem attributes of a planted forest on degraded pasturelands, Luquillo Experimental Forest

Ecosystem attribute	Outcome
Accumulated number of tree species	75 in 4.64 ha
Importance value of planted species	40 %
Importance value of introduced species	5 %
Aboveground carbon	80 Mg/ha
Soil carbon to 60 cm	102 Mg/ha
Fine root biomass	2.5 Mg/ha
Dead fine root biomass	2.3 Mg/ha
Live fine root biomass	0.1 Mg/ha
Rate of increase in forest soil carbon	0.9 Mg/ha.yr
Rate of loss of pasture soil carbon	0.4 Mg/ha.yr
Net rate of soil carbon accumulation	0.5 Mg/ha.yr
Net aboveground biomass accumulation	1.4 Mg/ha.yr
Fine root biomass accumulation	0.09 Mg/ha.yr
Litterfall	10–12 Mg/ha.yr

The forest was initially planted in the mid- to late 1930s with 13 tree species (nine native and four introduced). The outcome after 61 years is from Silver et al. (2004). Trees with diameter at breast height > 9.1 cm were measured. Importance value is the sum of relative density, relative basal area, and frequency by species based on 116 plots and expressed in percent

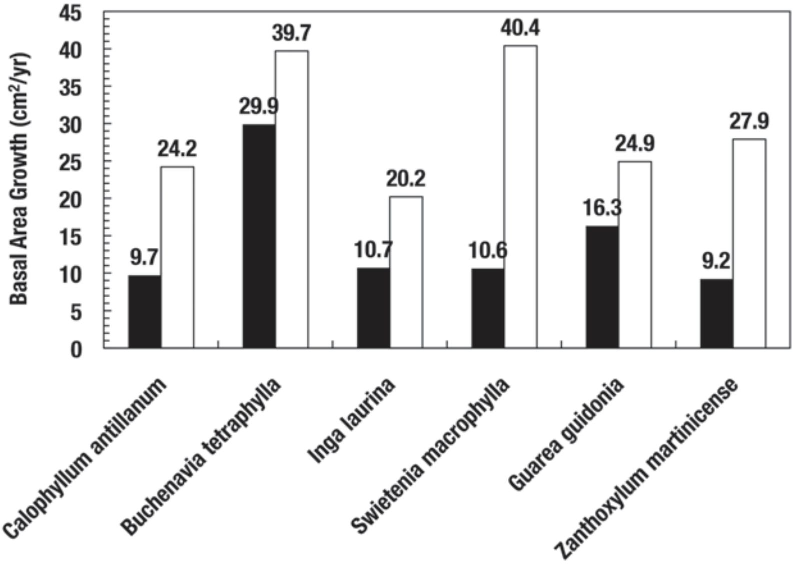

Fig. 19.9 Tree growth in a planted forest on degraded pasturelands, Luquillo Experimental Forest. The *solid bar* corresponds to the time interval of 1937–1959, and the *open bars* to the interval of 1959–1998. Data correspond to trees with diameter at breast height > 9.1 cm. The increased rates during the second time interval were all significant at $p < .05$ (Silver et al. 2004). *Swietenia* is an introduced species while the others are native tree species

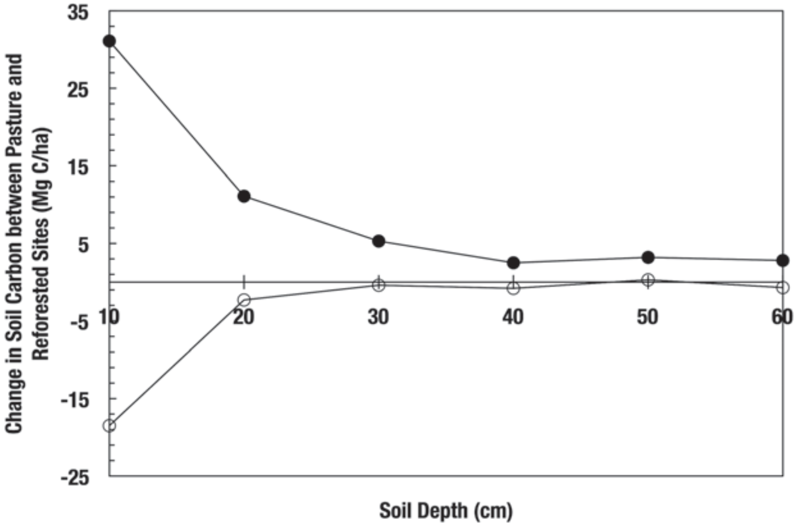

Fig. 19.10 Change in soil carbon over a period of 61 years in a planted forest on degraded pasturelands, Luquillo Experimental Forest. The data are based on stable isotope determinations (^{13}C and ^{12}C) whereby the soil carbon attributed to forests (C3, *solid points*) and grasses (C4, *open points*) is tracked through a 60 cm deep soil profile. (Details in Silver et al. 2004)

even if planted seldom, invade closed canopy native forests in the LEF. Some introduced animals like rats, mongooses, toads, mosquitoes, and bees do invade and establish populations in pristine forest stands at LEF, but they do not attain high abundances. In fact, introduced rats have been present in the forest for centuries and now appear naturalized at about 40/ha (Odum et al. 1970b). Odum et al. (1970b) assessed the situation thusly (p E-14): "There may be a pattern to finding the abundant, dominant, species of mans' farms and houses present in the rain forest as a scarce specialist there…."

In the restored forests on degraded pasturelands (above), introduced trees survived and reproduced after 62 years of succession, but they lost importance relative to native species over the long term. Thompson et al. (2007) examined the long-term dynamics of introduced species that are common in tabonuco forest recovering from past human activity. When people inhabited these sites, they planted trees for food, shade, or crops and many of these species are commonly seen in these recovering forests. The study was conducted in a 16-ha plot where all trees from > 1 cm have been tagged, identified, and measured. A hurricane affected the plot 1 year before the first inventory and also between the second and third inventory, which allowed the assessment of the influence of a natural disturbance on the dynamic of introduced species in closed canopy tabonuco forests. The following are the findings of Thompson et al. (2007) who analyzed population trends for 12 introduced tree species in the plot:

- Most introduced species were planted prior to 1932.
- As a group, introduced species constituted a small component of the stand, i.e., < 7 individuals/ha and < 1.6 m^2/ha (representing < 1 % of the stands basal area).

- Introduced species had lower mortality rates than native ones, and similar growth rates.
- The populations of four introduced species changed little over time.
- The populations of six introduced species declined between the first and second census, but increased after the hurricane.
- The population of one introduced species increased somewhat on all censuses and the population of another introduced species declined on all censuses.
- The populations of two introduced species increased under a closed canopy in areas that had a history of past anthropogenic disturbance.
- Most introduced populations have not migrated from where they were initially planted.

In summary, it appears that recurrent natural disturbances open the forest canopy and allow some regeneration of introduced species. However, the population density of these introduced species is low and as soon as the canopy closes, many individuals die, and the populations of introduced species do not increase, remaining at low densities, as do introduced animal species in the LEF.

Odum (1970) said it best (p I-275):

> When exotic organisms are introduced into a rain forest, the niche they can occupy is small and their role is that of a specialist; but, when the forest system is eliminated, the exotic may become the dominant since its programs of control are absent or left behind. Widespread destruction of native forest systems creating disturbance ecosystems allows invasions and upsets, which unharnessed may become epidemic, affecting desired trees, agricultural productions, etc. Some compromise with diversity may reduce the problem of disturbance from weed species. As discussed in connection with viruses and the *Aedes aegyptii* in the forest… diverse native forest may protect exotics as minor components and reservoirs for enormous multiplication potential. Irradiation and human disturbance of the El Verde forest seemed to develop mosquitoes and viruses. Straight control by killing is difficult, since to destroy the last reservoir or the undesired species would require disturbance of the natural forest reservoir thus increasing the situation favorable to the undesired species. The patterns for these organisms are like that of forest man who also has potential for dominance after the forest is cut but who is a protected minor component of the climax forest.

Earlier we discussed the carbon sink function of a planted forest on degraded pastureland in the LEF (Silver et al. 2004). The planting included 4 introduced tree species out of 13 that were planted and, within 61 years, the forest had 75 tree species. Of those species, introduced ones comprised 10.9% of the importance value (5% accounted by the planted species and the rest by one that was not planted), but two of the introduced species were in the top ten species and one ranked fourth in importance with a 5.9%. This species (*Syzygium jambos*) arrived to the plots by natural dispersal.

The species composition of this planted forest is new to Puerto Rico, as it includes introduced species and proportions of species that have not occurred in the island before. Hobbs et al. (2006) and Lugo and Helmer (2004) termed these new communities novel forests. It appears that these novel forests are a natural response to anthropogenic effects as the novelty of the species combinations is more dramatic as site degradation increases. The extremes occur outside of the LEF, where monocultures of introduced species colonize for discrete periods of time abandoned and degraded agricultural lands (Lugo 2004). After several decades, what appeared as a monoculture diversifies into new combinations of native and introduced species, much as was documented in the LEF by Silver et al. (2004).

19.10 Conclusions, Social Implications, and Research Networking

Research in the Luquillo Experimental Forest illustrates many examples of anthropogenic and natural disturbances and recovery events leading to successional pathways with different speeds and different species outcomes (Fig. 19.2), even if the end states are forests with similar structural characteristics. When the disturbances lead to arrested successions, the forest recovery process can be restarted by planting trees on abandoned pasture lands, which eventually not only leads to a net carbon sink aboveground and belowground but also provides habitat that facilitates colonization by native trees species that otherwise could not have so quickly established and dominated in abandoned pastures. Forest biomass and structure can recover quickly after hurricanes and localized disturbances such as forest road construction particularly when there is adjacent forest that can provide seed sources and organic matter inputs. The resilience of tabonuco forest to various types of disturbances is evidenced by the recovery of biomass and structure, but species composition does not recover in the same way. The apparent trade-off to this recovery is that the recovered forest produces new combination of species not observed previously. These new combinations of tree species are part of the response to disturbance, and part of the new successional trajectories created. Detailed observations on tree canopy dynamics and natural variation in growth rates of forest trees led to the application of the basal area reduction experiments that resulted in improvements of wood tree production in the tropics. This approach maintains only a few trees maturing concurrently for harvest, and this allows for management and harvest of other forest products to be possible.

In the LEF, the continuous and long-term monitoring of forest ecosystem components and processes, climate, and hydrology has been the basis for developing practical approaches to deal with watershed management needs at local and regional scales, and these also have potential for wider application. The impetus for much of this research was the dire social situation in Puerto Rico during the first half of the twentieth century. Overpopulation, an agrarian society, and dependency on fuelwood led to dramatic deforestation and land degradation, with the resulting environmental and social problems that develop when forest cover is lost on a moist tropical climate. The suite of disturbances afflicting forests, and depicted in Fig. 19.2, led to the long-term studies summarized here. The development of an experimental infrastructure in the LEF in turn led to an impressive array of collaborative work worldwide (Table 19.5). These collaborations plus the basic forestry research conducted over the past 100 years at the site contribute to improving understanding of these complex forests and to management actions designed to sustain forest productivity and resilience under constantly changing environmental conditions.

Table 19.5 Selected collaborative research and inter-site projects conducted at the Luquillo Experimental Forest (LEF) as part of collaborative research among experimental forests and ranges and experimental watersheds and with other research networks. (Information compiled by E. Meléndez Colóm, available at http://luq.lternet.edu/research/CrossSiteStudies and http://luq.lternet.edu/research/LTERProjectsList2)

Activity	Description
Luquillo Critical Zone Observatory, LCZO	The overarching focus of the LCZO is how critical zone processes and water balances differ in landscapes with contrasting bedrock but similar climatic and environmental histories. Sampling sites and a unified data management system will allow critical zone processes to be contrasted by bedrock, landscape position, depth, forest type, and location. https://criticalzone.org/luquillo/
Water in a changing environment	Research on impacts of climate change and variability on water supply from forested watersheds. Caspar Creek, Coweeta, Fraser, Fernow, H.J. Andrews, Hubbard Brook, LEF, Marcell, Santee, and San Dimas and other experimental watersheds
Experimental Forests and Ranges, International Cooperation Program (ICP) Level II	The EFR as a network established 18 sites to conduct the ICP level II climate and atmospheric monitoring. Each site will monitor climate parameters, atmospheric deposition, and ozone
Vegetation net productivity responses to precipitation variability	Collaboration among USDA ARS, USDA Southwest Watershed Research Center, University of Arizona, University of Technology Sydney, USDA-FS Northern Research Station, USDA Northwest Watershed Research Center, USDA-FS Pacific Southwest Research Station, and USDA-FS International Institute of Tropical Forestry
Water, Energy, and Biogeochemical Budgets, WEBB	This project compares the energy, water, and chemical budgets between forested basins in the Luquillo Experimental Forest and agriculturally developed basins. http://pr.water.usgs.gov/public/webb/
National Atmospheric Deposition Program, NADP	Precipitation chemistry data from El Verde, site PR20, at the LEF since 1985. http://nadp.sws.uiuc.edu/sites/siteinfo.asp?id=PR20&net=NTN
Relationship between nutrient inputs, faunal diversity, and abundance	Dominica, Saba, Costa Rica, Brazil, LEF
Long-term Intersite Decomposition Experiment Team, LIDET	The LIDET experiment is designed to test the effects of substrate quality and macroclimate on long-term decomposition and nutrient release dynamics of fine litter. 27 LTER and international sites http://knb.ecoinformatics.org/knb/metacat/nceas.328.26/knb
Tropical Montane Cloud Forest Network	Volunteer network of sites worldwide, United Nations Environment Programme, UNEP
Tropical nutrient limitation studies	LEF, Guánica, La Selva, Monte Verde, Barro Colorado Island, Tapajós, 64 sites total
Lotic Intersite Nitrogen Experiment, LINX	10 LTER and other sites, http://www.biol.vt.edu/faculty/webster/linx/

Table 19.5 (continued)

Activity	Description
Luquillo Forest Dynamics Plot, LFDP	The LFDP, previously known as the Hurricane Recovery Plot and the Luquillo long-term ecological research grid, is a 16-ha forest plot located near El Verde Field Station. Information from the LFDP contributes to the efforts of the Center for Tropical Forest Science (CTFS, Smithsonian Institution) network of large tropical forest plots in order to improve our understanding of tropical forests, to elucidate tree life histories, species interactions, and population changes in order to determine the forest response to environmental changes and disturbance. LEF + 17 tropical sites
Carbon, nitrogen, and phosphorus dynamics in tropical forest ecosystems	LEF, Tapajós, Brazil
Dissimilatory nitrate reduction in humid ecosystems	LEF, Bonanza Creek Experimental Forest, La Selva
Comparative study of terrestrial and aquatic decomposition rates	LEF, Coweeta Hydrologic Laboratory
Earthworms and soil processes in tropical ecosystems	LEF, Xishuangbanna, China
World Wide Aquatic Leaf Decomposition Experiment, WW-DECOEX	LEF + 10 tropical sites
Comparisons of hydrology, nutrient cycling, and canopy dynamics following severe storm damage	LEF, Hubbard Brook Experimental Forest, Taiwan
Comparison of bromeliad phytotelmata in tabonuco and elfin forests	LEF, Dominica
Network analysis of food webs	LEF and six LTER sites
UNESCO Help Program	LEF, 12 watersheds in the USA, including H. J. Andrews Experimental Forest and others worldwide
Landscape fragmentation and forest fuel accumulation: effects of fragment size, age, and climate	LEF, Bonanza Creek Experimental Forest, Idaho
Comparison of aquatic insect emergence	LEF, La Selva, Costa Rica

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References

Benstead JP, March JG, Pringle CM (2000) Estuarine larval development and upstream postlarval migration of freshwater shrimps in two tropical rivers, Puerto Rico. Biotropica 32(3):545–548

Blanco JF, Scatena FN (2006) Hierarchical contribution of river-ocean connectivity, water chemistry, hydraulics, and substrate to the distribution of diadromous snails in Puerto Rican streams. J N Am Benthol Soc 25(1):82–98

Brokaw N, Fraver S, Grear JS, Thompson J, Zimmerman JK, Waide RB, Everham-III EM, Hubbell SP, Foster RB (2004) Disturbance and canopy structure in two tropical forests. In Losos E, Leigh EG Jr (eds) Tropical forest diversity and dynamism: results from a long-term tropical forest network. University of Chicago Press, Chicago, pp 177–194

Brown S, Lugo AE, Silander S, Liegel L (1983) Research history and opportunities in the Luquillo Experimental Forest. USDA Forest Service, Southern Forest Experiment Station, General Technical Report SO-44, New Orleans, LA

Covich AP (2006) Dispersal-limited biodiversity of tropical insular streams. Polish J Ecol 54:523–547

Covich AP, McDowell WH (1996) The stream community. In: Reagan DP, Waide RB (eds) The food web of a tropical rain forest, Chap. 13. University of Chicago, Chicago, pp 434–459

Covich AP, Crowl TA, Johnson SL, Varza D, Certain D (1991) Post-Hurricane Hugo increases in atyid shrimp abundances in a Puerto Rican montane streams. Biotropica 23:448–454

Covich AP, Crowl TA, Johnson SL, Pyron M (1996) Distribution and abundance of tropical freshwater shrimp along a stream corridor: response to disturbance. Biotropica 28:484–492

Covich AP, Crowl TA, Scatena FN (2003) Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. Freshw Biol 48:1199–1206

Covich AP, Crowl TA, Heartsill Scalley T (2006) Effects of drought and hurricane disturbances on headwater distributions of palaemonid river shrimp (*Macrobrachium* spp.) in the Luquillo Mountains, Puerto Rico. J N Am Benthol Soc 25:99–107

Covich AP, Crowl TA, Hein CL, Townsend MJ, McDowell WH (2009) Importance of geomorphic barriers to predator-prey interactions in river networks. Freshw Biol 54:450–465

Cross WF, Covich AP, Crowl TA, Benstead JP, Ramirez A (2008) Secondary production, longevity, and consumption rates of freshwater shrimps in two tropical streams with contrasting geomorphology and foodweb structure. Freshw Biol 53:2504–2519

Crowl TA, Covich AP (1994) Responses of a freshwater shrimp to chemical and tactile stimuli from a large decapod predator. J N Am Benthol Soc 13:291–298

Crowl TA, Welsh V, Heartsill Scalley T, Covich AP (2006) Effects of different types of conditioning on rates of leaf-litter shredding by *Xiphocaris elongata*, a Neotropical freshwater shrimp. J N Am Benthol Soc 25(1):198–208

Dowler CC, Tschirley FH (1970) Effects of herbicides on a Puerto Rican rain forest. In: Odum HT, Pigeon RF (eds) A tropical rain forest. National Technical Information Service

Drew AP, Boley JD, Zhao Y, Johnston MH, Wadsworth FH (2009) Sixty-two years of change in subtropical wet forest structure and composition at El Verde, Puerto Rico. Interciencia 34(1):34–40

Gentry AH (1982) Patterns of neotropical plant species diversity. Evol Biol 15:1–83

Guariguata MR (1990) Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. J Ecol 78:814–832

Heartsill Scalley T, Scatena FN, Estrada C, McDowell WH, Lugo AE (2007) Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico. J Hydrol 333:472–485

Heartsill Scalley T, Scatena FN, Lugo AE, Moya S, Estrada C (2010) Changes in structure, composition and nutrients during 15 year of hurricane-induced succession in a subtropical wet forest in Puerto Rico. Biotropica. doi:10.1111/j.1744-7429.2009.00609.x

Heyne CM (2000) Soil and vegetation recovery on abandoned paved roads in a humid tropical rain forest, Puerto Rico. Department of Biological Sciences. Las Vegas, USA, University of Nevada. 153 p

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vilà M, Zamora R, Zobel M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob Ecol Biogeogr 15:1–7

Holdridge LR (1967) Life zone ecology. Tropical Science Center, San José

Hutchinson ID, Wadsworth FH (2006) Efectos de la liberación en un bosque secundario de Costa Rica. Recs. Nats. y Amb. 46:155–160

Kharecha P (1997) Energy evaluation of the effects of human activities on the Luquillo Experimental Forest, Puerto Rico. M.S. thesis in Center for Environmental Policy and Environmental Engineering Sciences. University of Florida, Gainesville, 39 p

Kikkert DA, Crowl TA, Covich AP (2009) Upstream migration of amphidromous shrimp in the Luquillo Experimental Forest, Puerto Rico: temporal patterns and environmental cues. J N Am Benthol Soc 28:233–246

Lugo AE (1986) Water and the ecosystems of the Luquillo Experimental Forest. USDA Forest Service, Southern Forest Experiment Station General Technical Report SO-63, New Orleans, LA

Lugo AE (1994) Preservation of primary forests in the Luquillo Mountains, Puerto Rico. Conserv Biol 8:1122–1131

Lugo AE (2004) The outcome of alien tree invasions in Puerto Rico. Front Ecol Environ 2:265–273

Lugo AE (2005) Los bosques. In: Joglar RL (ed) Biodiversidad de Puerto Rico. Vertebrados terrestres y ecosistemas. Editorial del Instituto de Cultura Puertorriqueña, San Juan, pp 395–548

Lugo AE (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international review. Austral Ecol 33:368–398

Lugo AE, Scatena FN (1995) Ecosystem-level properties of the Luquillo Experimental Forest with emphasis on the tabonuco forest. In: Lugo AE, Lowe C (eds) Tropical forests: management and ecology. Springer, New York, pp 59–108

Lugo AE, Scatena FN (1996) Background and catastrophic tree mortality in tropical moist, wet, and rain forests. Biotropica 28:585–599

Lugo AE, Helmer E (2004) Emerging forests on abandoned land: Puerto Rico's new forests. For Ecol Manag 190(2):145–161

March JG, Benstead JP, Pringle CM, Scatena FN (2003) Damming tropical island streams: problems, solutions, and alternatives. Bioscience 53(11):1069–1078

Marrero J (1950) La reforestación de tierras degradadas de Puerto Rico. Caribb For 11:16–24

Murphy PG (1970) Tree growth at El Verde and the effects of ionizing radiation. In: Odum HT, Pigeon RF (eds) A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. National Technical Information Service, Springfield, pp D141–D171

Odum HT (1970) Summary: an emerging view of the ecological systems at El Verde. In: Odum HT, Pigeon RF (eds) A tropical rain forest. National Technical Information Service, Springfield, pp I191–I289

Odum HT, Drewry G (1970) The cesium source at El Verde. In: Odum HT, Pigeon RF (eds) A tropical rain forest. National Technical Information Service, Springfield, pp C23–C36

Odum HT, Murphy P, Drewry G, McCormick F, Schinham C, Morales E, McIntyre J (1970a) Effects of gamma radiation on the forest at El Verde. In: Odum HT, Pigeon RF (eds) A tropical rain forest. National Technical Information Service, Springfield, pp D3–D75

Odum HT, Drewry G, McMahan EA (1970b) Introduction to section E. In: Odum HT, Pigeon RF (eds) A tropical rain forest. National Technical Information Service, Springfield, pp E3–E15

Olander L, Scatena FN, Silver WL (1998) Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. For Ecol Manag 109:33–49

Parresol BR (1995) Basal area growth for 15 tropical tree species in Puerto Rico. For Ecol Manag 73:211–219

Parrotta JA (1999) Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. For Ecol Manag 124:45–77

Scatena FN (2001) Ecological rhythms and the management of humid tropical forests: examples from the Caribbean National Forest, Puerto Rico. For Ecol Manag 55(28):1–12

Scatena FN, Moya S, Estrada C, Chinea JD (1996) The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica 28:424–440

Schimper AFW (1903) Plant-geography upon a physiological basis. Clarendon, Oxford
Silver WL, Scatena FN, Johnson AH, Siccama TG, Watt F (1996) At what temporal scales does disturbance affect below ground nutrient pools? Biotropica 28(Special Issue 4a):441–458
Silver WL, Kueppers LM, Lugo AE, Ostertag R, Matzek V (2004) Carbon sequestration and plant community dynamics following reforestation of tropical pasture. Ecol Appl 14:1115–1127
Smith RF (1970) The vegetation structure of a Puerto Rican rain forest before and after short-term gamma irradiation. In: Odum HT, Pigeon RF (eds) A tropical rain forest. National Technical Information Service, Springfield, pp D103–D140
Taylor CM, Silander S, Waide RB, Pfeiffer WJ (1995) Recovery of a tropical forest after gamma irradiation: a 23-year chronicle. In: Lugo AE, Lowe C (eds) Tropical forests: management and ecology. Springer, New York, pp 258–285
Thompson J, Lugo AE, Thomlinson J (2007) Land use history, hurricane disturbance, and introduced species survival in a subtropical wet forest in Puerto Rico. Plant Ecol 192:289–301
Wadsworth FH (1995) A forest research institution in the West Indies: the first 50 years. In: Lugo AE, Lowe C (eds) Tropical forests: management and ecology. Springer, New York, pp 33–56
Wadsworth FH (1997) Forest production for tropical America. USDA Forest Service, Washington, DC. (Agriculture Handbook 710)
Wadsworth FH, Zweede JC (2006) Liberation: acceptable production of tropical timber. For Ecol Manag 233:45–51
Wadsworth FH, Bryan B, Figueroa-Colón J (2010) Cutover tropical forest productivity potential merits assessment, Puerto Rico. Bois For Trop 305:33–41
Walker LR, Zarin DJ, Fetcher N, Myster RW, Johnson AH (1996) Ecosystem development and plant succession on landslides in the Caribbean. Biotropica 28:566–576
Weaver PL, Murphy PG (1990) Forest structure and productivity in Puerto Rico's Luquillo Mountains. Biotropica 22:69–82