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Review

On the Shoulders of Giants: Continuing the Legacy of Large-Scale Ecosystem Manipulation Experiments in Puerto Rico

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Abstract: There is a long history of experimental research in the Luquillo Experimental Forest in Puerto Rico. These experiments have addressed questions about biotic thresholds, assessed why communities vary along natural gradients, and have explored forest responses to a range of both anthropogenic and non-anthropogenic disturbances. Combined, these studies cover many of the major disturbances that affect tropical forests around the world and span a wide range of topics, including the effects of forest thinning, ionizing radiation, hurricane disturbance, nitrogen deposition, drought, and global warming. These invaluable studies have greatly enhanced our understanding of tropical forest function under different disturbance regimes and informed the development of management strategies. Here we summarize the major field experiments that have occurred within the Luquillo Experimental Forest. Taken together, results from the major experiments conducted in the Luquillo Experimental Forest demonstrate a high resilience of Puerto Rico's tropical forests to a variety of stressors.

Keywords: Luquillo Experimental Forest; tropical; experiments; manipulations; large-scale; Puerto Rico; Caribbean

1. Introduction

The Luquillo Experimental Forest, located in the northeastern corner of Puerto Rico (18° N, 66° W), is one of the oldest reserves in the Western Hemisphere [1] (Figure 1). In 1876, King Alphonso XII proclaimed 10,000 hectares within the Luquillo Mountains a reserve of the Spanish Crown. Just 22 years later, Spain ceded control of the forest to the United States as part of the Treaty of Paris in 1898, and in 1903, President Theodore Roosevelt designated the area a forest reserve under the jurisdiction of what is now the U.S. Department of Agriculture (USDA) Forest Service [1]. The broad diversity of climate, geology, and flora and fauna found within the Luquillo Experimental Forest has attracted a wide range of ecological research throughout its history [1–4]. Within an area of what is now just over 11,000 ha, the elevation spans 100 to 1075 m asl. Across this change in elevation, mean annual rainfall spans 2450 to 4000 mm and average monthly air temperature ranges between 23.5 and 27 °C at lower elevations and 17 and 20 °C at the higher elevations [5]. There are two major bedrocks (marine volcaniclastic and intrusive igneous rocks from the Cretaceous and Tertiary periods), and three major soil orders (Ultisol, Inceptisol, Oxisol) within the Luquillo Experimental Forest [4]. The forest is also highly diverse with 164 animal species (24 endemic), more than 1000 plant species, and 224 tree species (60 endemic) [4]. In light of this range of conditions, it is no surprise that there are five Holdrige life zones found within the Luquillo Experimental Forest: wet forest, rain forest, lower montane wet forest, lower montane rain forest, and a small area in the southwest region that is moist forest life zone [2].

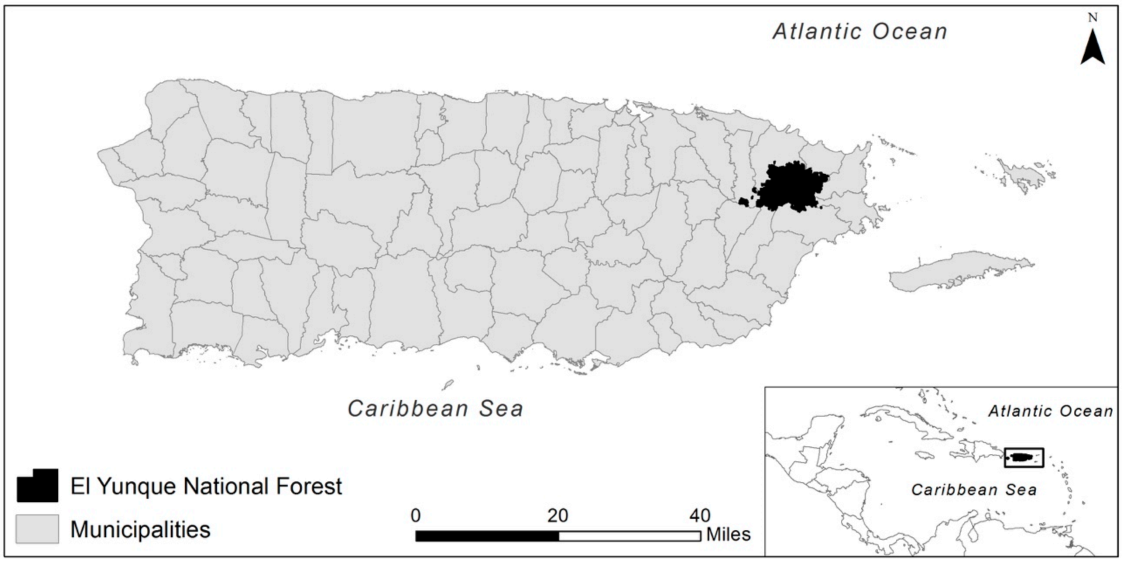

Figure 1. Map of Puerto Rico and the location of the Luquillo Experimental Forest.

Long-term monitoring within the Luquillo Experimental Forest includes assessment of factors such as climate, forest composition, and biomass, and these observations have been a part of the Luquillo Experimental Forest since the early 1900's [1,2]. This long-term monitoring has been critical to establishing fundamental knowledge of the forest system, allowing us to understand basic seasonal patterns, capture the ebbs and flow of forest composition, and to explore the potential for slower, directional changes that might otherwise be missed. However, society often demands answers on timescales much faster than long-term research can provide. While manipulative experiments have numerous challenges [6,7], they nevertheless enable researchers to isolate the effects of changes to individual variables so that we can test mechanistic hypotheses on a more feasible timescale and thus better anticipate the needs, follies, wants, and dreams of man, that are likely to affect the environments of the planet [8]. The manipulative experimental approach can additionally be used to reveal important insights about system responses to extreme, infrequent, or abrupt events [9], thus providing essential insights for societies that must develop coping strategies and management plans for such events.

Throughout its history, the use of and experiments conducted within the Luquillo Experimental Forest have been a reflection of the times. From the early foresters that explored forest management techniques in the 1900's [1] to the more recent large-scale field manipulation experiments [10], these studies provide a window into the greatest interests and concerns of society. The objective of this article is to synthesize the history of field manipulation experiments within the Luquillo Experimental Forest, beginning with the early days of U.S. jurisdiction of the forest. We aim to place these experiments into historical context and to evaluate their contribution to our greater understanding of tropical forest ecology. To understand where we are and where we are going, it is important to take time to reflect on where we have been. As Isaac Newton so aptly said, "If I have seen further, it is by standing on the shoulders of giants [11]".

In the early days of the Luquillo Experimental Forest, the U.S. was keenly interested in maximizing the ability to reforest degraded landscapes and to cultivate and manage forests. In response to this need, the USDA Forest Service began silvicultural experiments on the island of Puerto Rico. Tree plantations were established throughout the Luquillo Experimental Forest from the early 1930's to the late 1950's, and studies of secondary forest succession and forest management practices were implemented [12–14]. Thus began the methodical assessment of the commercial value of timber and the experimentation of forest management practices, such as forest thinning, to promote forest growth. In the 1960's, the development of nuclear technology was well under way and the need for a greater understanding of how radiation exposure might affect our nation's biological resources was recognized [15]. At the same time, scientists were interested in our ability to quantify whole-forest metabolism. With these motivating factors in mind, scientists developed studies of whole-forest energetics [16], evaluated the effects of herbicides [17–19], and implemented one of the three gamma radiation studies conducted in forests in the United States [20]. In 1989 Hurricane Hugo passed over the island of Puerto Rico [21], followed by Hurricane Georges in 1998 [22], which spurred a wealth of research surrounding the effects of hurricanes on forest recovery [22–25]. This included experiments that simulated key aspects of hurricane disturbance, such as debris deposition, at smaller scales [26,27]. In the 21st Century, anthropogenic change and changes to climate emerged as some of the most important research needs of our time. This growing interest in understanding the effects of both long-term directional change and repeated, cyclical disturbance on forest recovery led to the establishment of a wealth of experimental studies, including a clear cutting experiment [28,29], a nitrogen (N) deposition experiment [30], rainfall manipulation studies [31,32], and a forest warming experiment [10]. While there remains much to learn, the Luquillo Experimental Forest represents one of the longest and best-studied tropical forests in the world. Together, the history and wealth of experimental research in the Luquillo Experimental Forest has formulated a greater understanding of tropical forests and their resilience to environmental change, the depth of which has literally filled volumes of books [2,20,33–37]. Below, we highlight the varied and impressive history of manipulation experiments that have taken place within the Luquillo Experimental Forest and provide a general summary of the major conclusions and contributions of each of these studies and their contribution to current understanding.

2. Field Manipulation Experiments in the Luquillo Experimental Forest

2.1. *Silviculture (1930s–Today)*

By the late 1920's Puerto Rico was largely deforested [38], with descriptions of a landscape that supported "eroded soils, denuded forest areas, sedimented rivers and reservoirs, reduced soil fertility, low crop yields, and an inadequately fed people" [39]. However, following two major hurricanes in 1928 and 1932 combined with a series of economic setbacks, Puerto Rico saw a massive abandonment of agricultural lands as people moved to the cities for work [38]. As a result, much of the island in Puerto Rico entered into early stages of forest succession by the late 1930's [38]. During this period (1933 and 1949) the USDA Forest Service added large amounts of land in the areas surrounding the Luquillo Experimental Forest, in what amounts to approximately 50% of the Luquillo Experimental Forest today [1]. As such, one of the early objectives of the USDA Forest Service was to develop reforestation programs, promote tree growth and cultivate plantation forestry in the tropics. From the early 1930's to the late 1940's more than 1500 hectares of tree plantations were established across the island [12]. These initial tree plantings included mahogany (*Swietenia macrophylla*) plantations that still grace the Luquillo Experimental Forest today [1]. In 1942, Frank H. Wadsworth, who was to become the Director of the now USDA Forest Service International Institute of Tropical Forestry from 1953 to 1979, arrived in Puerto Rico. In the coming years, Wadsworth would pioneer tropical forestry management and conservation on the island. In 1943 he began establishing a series of 420 0.1 ha plots across the Luquillo Experimental Forest, which ranged from 200 m to 640 m elevation. Plots along this elevation gradient were created in preparation for the development of a land management plan and to satisfy his interest in understanding how trees grow in complex forests [40]. All trees with diameter at breast height of greater than 9.1 cm were tagged, measured, and identified to species. These plots have been re-measured at various points in time from 1947 to present, providing a baseline for understanding the growth and productivity of thousands of trees within the Luquillo Experimental

Forest over a 75-year period [41–47], and a critical foundation against which experimental results have be compared [15,40,48,49].

Around this time, the United States was entering a post-war energy crisis. In response, Wadsworth established new plots in 1945 to evaluate and develop timber management practices. In a portion of these plots, 50% of basal area was removed, which showed that thinning does indeed increase the growth of the remaining trees [3]. Wadsworth later (1957) established approximately 100 0.08 hectare plots across two lower elevation forests, which included a secondary forest and an old growth forest site. In these plots, the commercially valuable trees were marked and measured while the poorest growing trees were removed as part of a pilot management project designed to increase productivity by providing greater canopy freedom [42]. In 1975, 40 of these plots were re-measured. Surprisingly, very little difference between the mean growth rates in these plots versus the old growth forest stands was observed [42]. However, closer analyses of growth data from the various plots established by Wadsworth have revealed the importance of canopy crown diameter and position for determining growth potential [42,45]. The long-term experiment yielded a wide range of plant species that varied within and across plots, and thus the sites were subsequently used to explore the role of biodiversity in ecosystem processes [42,45,50,51]. The known age and composition of the plots, together with the fact that many were established on abandoned pasture land, facilitated the study of long-term carbon dynamics. The sites were resurveyed in 1992, and a subset re-measured in the early 2000's to determine biomass change and soil carbon dynamics with reforestation. Stable carbon isotopes were used to track the soil carbon change over time, giving one of the first estimates of soil carbon gain and loss with tropical reforestation [41]. The initial studies were revolutionary. They represent the first silviculture studies conducted anywhere in Latin America, and are an invaluable resource for long-term research. Many of the tree plantations and experimental plots established by Wadsworth and the International Institute of Tropical Forestry are still present in Puerto Rico today. They serve as the oldest established research plots for evaluating tree growth and production in the forest, providing a baseline for understanding contemporary responses of the Luquillo Experimental Forest to long-term directional changes in climate, and in cyclical disturbance events, such as hurricanes [2,40,43,44,46,48].

2.2. Forest Radiation Experiment (1963–1968)

In the 1960's, nuclear technology was expanding beyond its use for military purposes to include domestic applications such as nuclear energy and excavation of large areas. In particular, the U.S. was considering using a nuclear device for excavating a second Panama Canal between the Pacific and Atlantic Oceans [15]. Earlier radiation experiments conducted in temperate forests in Brookhaven, New York and Dawsonville, Georgia [52] revealed high mortality of pine trees, alleviating the perception that plants were likely resistant to radiation [20]. It thus became apparent that assessments of the consequences of atomic evacuation, nuclear war, and atomic accidents should include effects on natural ecosystems as well as the effects on humans. Scientists recognized that responses to radiation might vary by ecosystem, particularly in lower latitudes, which support highly diverse forests with complex structure [15]. Thus, the Atomic Energy Commission (now the U.S. Department of Energy) funded a 5-year study in 1963 to investigate the effects of radiation on forest processes in the Luquillo Experimental Forest. The prevailing theory was that more complex organisms with larger nuclei would be more sensitive to radiation than less complex organisms with smaller nuclei due to the greater volume of deoxyribonucleic acid (DNA) in large nuclei [53]. It was further hypothesized that the rapid cycling in tropical forests would contribute to a faster response to radiation than what had been observed in temperate systems, and that species diversity and forest complexity were likely to be important factors [20]. To test this theory, a small area within the Luquillo Experimental Forest was exposed to almost continuous gamma radiation (10,000-curie Cesium-137 source; Figure 2) for 24 h a day over a 3-month period (19 January to 27 April, 1965) and was studied for a full year following exposure. Scientists measured the effects of radiation (stress) on plants, seedlings, and seed germination rates, animals, soils, microbes, mineral cycling, forest metabolism and energy flows.

Figure 2. Scientists installing the base and casing for the Cesium radiation source in the Luquillo Experimental Forest. Photo reproduced from [53].

The effects of radiation on the vegetation were not clearly discernable in the initial months following radiation exposure, and in fact, some scientists thought that the canopy leaves in the immediate vicinity of the radiation center might be greener than those nearby. Howard T. Odum, the lead scientist on the project, noted that radiation effects in these initial days were difficult to observe from aerial views, color photographs, and from a nearby mountain slope, despite everyone on the project making daily trips to see the change [53]. However, within a few months, areas within the line-of-site of the radiation source were obviously affected. The ground surrounding the source was bare of living green, moss on the nearby rocks turned a strange blue-black color, many of the surrounding trees began dropping green leaves, and there were observations of albino, chlorotic, and abnormally shaped leaves [53–55]. Scientists additionally noted that the leaves of a *Manilkara* tree close to the radiation center turned bright red before dropping. Radiation exposure also increased susceptibility to insect grazing in the initial months following radiation exposure. The number of leaf holes in the surrounding vegetation increased and bark beetles invaded the most heavily affected trees [53]. Within 7 months of radiation exposure, mortality of the most heavily affected individuals stabilized at less than 10% [55]. However, as the year progressed the canopy continued to open, and by the following year a small gap had opened up in the canopy. Ultimately the majority of trees within the 30-m radius of the radiation source died [28,54]. One of the most dominant plants within the Luquillo Experimental Forest, the sierra palm (*Prestoea montana*), was particularly sensitive to radiation with a 94% decline in population density in the areas surrounding the radiation center [29]. However, some trees were also resistant to radiation. A giant red-trunked *Cyrilla* tree 5-m north of the radiation source was exposed to 100,000 Roentgen of radiation [53]. It was permanently scarred on one side and lost more than half of its leaves; however, the tree survived another 33 years before it died during a major rain storm in 1998 [56].

A year after exposure to radiation, the forest reached the maximum extent of defoliation. It then took over a year for the spread of green cover to return [53]. Recovery of vegetation was found to be more rapid in areas that had been shielded from radiation by rocks and tree trunks [53]. Seedling growth eventually spread throughout the recovery center [57]. Secondary forest species were more resilient than old growth species, demonstrating overall greater resistance to radiation exposure [55]. When considering the multitude of observations following radiation exposure, it became clear that the initial hypothesis that radiation sensitivity would increase with nuclear volume did not hold. For example, the sierra palm (*Prestoea montana*) was much more sensitive to radiation exposure (smaller nuclei) than secondary forest species, which as a group had larger nuclei [53,55]. Forest structure was also considered important when evaluating radiation sensitivity, with more complex forests hypothesized to have greater sensitivity [52,55]. However, the radiation sensitivity of the Luquillo Experimental Forest, which is considered a more complex forest, relative to the response of temperate forests also exposed to radiation, found no particular difference in the response of the two forest types. Rather, they hypothesized that resistance to radiation of some species over others may be due to the simplicity of the physiology rather than the size of the nuclei, which could explain the resistance of the secondary species in the Luquillo Experimental Forest as well as the resistance of the herbaceous vegetation observed in the temperate forests [55].

Twenty-three years later, scientists revisited the radiation site and found slow recovery of the radiated forest relative to natural gaps, as well as an overall loss of seeds in the soil [28]. Scientists have additionally found that the rate of biomass recovery following radiation was much slower than that of biomass recovery following hurricane disturbance and that the depressed recovery has continued to persist in the radiated site as long as 44 years following irradiation [40]. Whether this stunted recovery following radiation exposure is microbially controlled, or due to substantial loss of the seed bank is not clear. While the implementation of the radiation study in the Luquillo Experimental Forest is controversial to this day, at the time it was the most comprehensive study of a tropical forest ever conducted, making the Luquillo Experimental Forest one of the earliest and best-studied tropical forests in the world. Odum used the radiation experiment as an opportunity to study everything he could about the forest [20]. He pioneered studies on ecosystem function and the forest's connections to global cycles of energy, water, nutrients, and carbon, and the resulting book volume compiled by Odum [20], serves as a central reference for scientists studying the Luquillo Experimental Forest to this day.

2.3. Rain Forest Herbicide Experiment (1964–1965)

In the mid-1960's U.S. involvement in the Vietnam War was escalating. Deployment of troops increased from 760 in 1959 to 23,300 in 1964, and reached over 500,000 troops by 1968 (U.S. Department of Defense Manpower Data Center). As a military tactic, the US began using the "Rainbow" herbicides (herbicide mixtures named by the colored identification band painted on their storage barrels), such as Agent Orange, in 1961 to defoliate forests and mangroves, to clear perimeters of military installations and to destroy 'unfriendly' crops as a tactic for decreasing cover and food supplies for the enemy [58]. By 1965 the U.S. had applied approximately two million liters of herbicides in the Republic of Vietnam [58]. In the midst of these events, the USDA Crops Research led a series of herbicide experiments in the Luquillo Experimental Forest from 1964–1965 that were funded by the U.S. Department of Defense Advanced Research Projects Agency. The Department of Army personnel determined that the forests in the Luquillo Experimental Forest were similar to the evergreen forests of Southeast Asia. Thus, tactical herbicides capable of defoliating the tropical vegetation of the Luquillo Experimental Forest could be applied to Southeast Asian forests to reduce the amount of obscuring vegetation, which would reduce the possibility of ambush, and increase the ability to observe the movement of enemy equipment [59].

In January 1964, scientists applied six herbicides (picloram, prometone, bromacil, dicamba, fenac, diuron) to forest soils with a cyclone seeder at rates of 3.7, 10 and 30 kg per ha. They used a randomized complete block design with three replicates for a total of sixty-three 18 m $\times$ 24 m plots with 6 m buffers [19]. The effect of herbicide applied to the soils was evident within one month of application and maximum defoliation occurred nine-months post herbicide application [18]. Picloram, a major component of the rainbow herbicide Agent White, was the most effective herbicide, killing between 22% and 71% of vegetation 21 months after treatment [18]. Fenac was the most persistent herbicide in the soil [18], reaching soil depths of 91 to 122 cm within three months of application, suggesting substantial downward movement of herbicides into the soil profile [19]. Forest plant succession occurred within 18 months of herbicide application [19], and there was no effect on the composition of the species that regrew when compared with other secondary forest in the area [18].

Following the initial soil herbicide experiments, scientists explored the effects of foliar application, focusing on the most effective defoliant, picloram, which was applied in various combinations with two other herbicides, paraquat and pyriclor [18]. Foliar application occurred in October, 1965 in separate 0.4 ha plots (53 m $\times$ 76 m with a 15 m buffer) established in a randomized block design with two replicates. Herbicides were applied in liquid form at rates of between 6.7 and 20 kg per ha with a Hiller 12-E helicopter that flew in five 11 m swaths at treetop level over each plot. The effects of foliar application on defoliation were much more immediate than either the soil herbicide or the radiation treatments [18], with measurable effects within one week of application and maximum defoliation occurring three-months post-herbicide application (Figure 3). The resulting defoliation substantially affected the light environment and microclimate up to a year following treatment; however, as with soil herbicide application, the forest recovered relatively quickly, and the species composition of succession was not affected [18]. Several months after herbicide application, scientists planted mahogany and teak trees in numerous plots. Both tree species grew well and showed no signs of being affected by herbicides [18]. Thus, while the initial responses to herbicide application were immediate and dramatic, once the herbicides were flushed out of the soil rooting zone, the forest appeared to recover normally.

Overall, picloram proved to be an effective defoliant of trees in the Luquillo Experimental Forest, whether applied directly to the soil or to the vegetation. The relatively rapid rate of regeneration (within 1.5 years) following very high levels of herbicide application to the soil (up to 30 kg per ha) suggests that the effects of the herbicides in this forest are transient and unlikely to 'sterilize' the soil for long periods of time [18]. In addition, the composition of species that comprised initial forest succession following herbicide application did not appear to be affected, with no new 'invasive' species introduced during recovery [19]. Defoliation of the forest occurred more rapidly in response to herbicide application than what was observed in the radiation experiment [18]. At the same time, the forest also recovered from herbicide application at a much faster rate than from radiation exposure [28]. From a military perspective, Agent White, of which picloram is a major component, was found to be less advantageous than Agent Orange because defoliation took several weeks to begin [58]. However, due to changes in chemical market forces in the mid-1960's, Agent Orange production became limited and it was not available in sufficient supplies for military application. Thus, the U.S. transitioned to the use of Agent White in 1966, applying an estimated total of 20,556,525 liters to the forests of the Republic of Vietnam from 1966–1971 [58].

Figure 3. Changes in canopy opening prior to and three months following herbicide application in the Luquillo Experimental Forest. Photograph reproduced from [18].

2.4. Giant Plastic Cylinder Study (1966–1967)

Also supported by the Atomic Energy Commission, Howard T. Odum established the "Giant Plastic Cylinder" study in 1966 in order to better understand whole-forest metabolism and fluxes of water, carbon, and energy [16]. A 17-m tall x 18 m wide plastic chamber (Figure 4) was erected in the Luquillo Experimental Forest with a 22-m canopy access tower in the center, enabling Odum and collaborators to study vertical gradients and partition fluxes into their various components. Six 17-m tall crank up aluminum towers were hauled up the mountain and installed in a hexagonal array on concrete pads with steel wire creating the frame. Plastic material that could be bonded with adhesive was pulled up to the wire frame to form a cylinder. This material lasted a year and a half under forest exposure, which limited the duration of the study [16]. Although the experiment ran for just over one year, the study was immensely valuable for understanding tropical forest function. This study was the first attempt at assessing whole-forest metabolism and provided initial estimates of tropical forest evapotranspiration, forest floor respiration, vertical gradients of photosynthesis, gross photosynthetic rates, leaf area index, and chlorophyll content, as well as an overall assessment of carbon dioxide fluxes. As a whole, the Giant Plastic Cylinder was a visionary prototype, and served as a precursor for future open top chamber and eddy covariance studies.

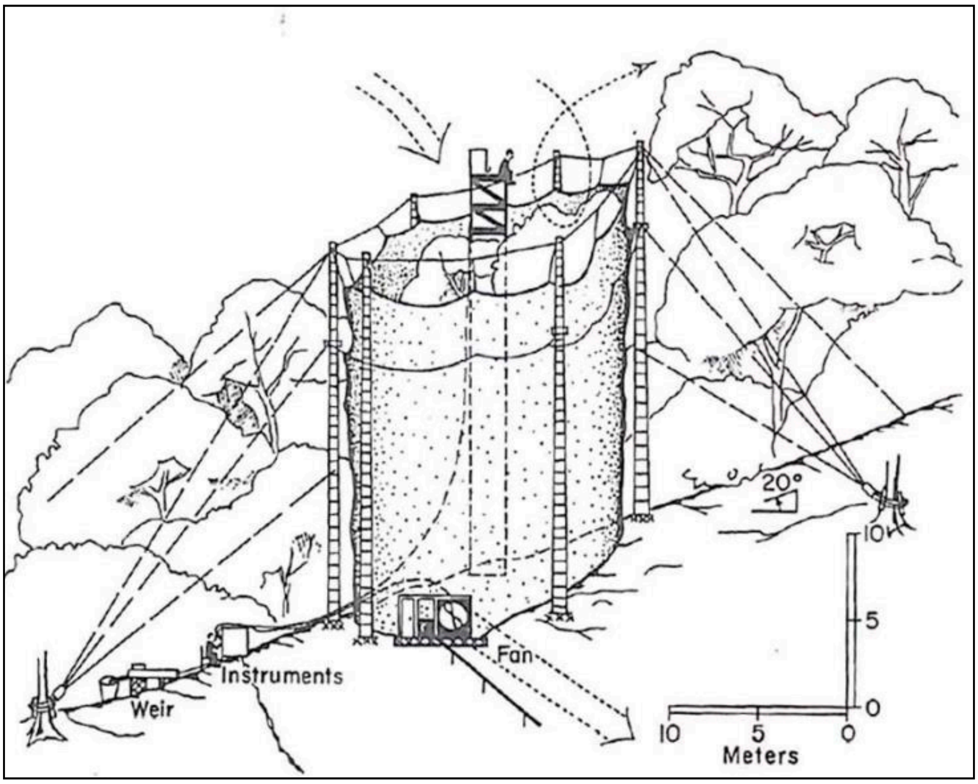

Figure 4. Schematic diagram of the Big Plastic Cylinder Experiment. Reproduced from [16].

2.5. The GAPS Experiment (1988-Today)

By the late 1970's scientists recognized that the area of secondary forests was increasing rapidly [60], and that with few exceptions most tropical countries had a larger land surface cover of secondary vegetation than old growth [61]. It was suggested that the tropics were entering the "era of secondary vegetation" [61]. At the time, studies of carbon dynamics in secondary forests were sparse [60], and to date, most studies have focused on successional changes in vegetation and the drivers, patterns, and consequences of deforestation at large spatial scales [60,62,63]. Fewer studies have followed the *in-situ* biogeochemical effects of deforestation and forest regrowth over time [64]. In 1988, scientists established an experiment to determine the carbon and nutrients effects of tropical deforestation, and to follow soil biogeochemical dynamics and patterns in forest regrowth over time. Three 32 m × 32 m plots (two treatment plots and a split control plot) were established in the Bisley Research Watersheds of the Luquillo Experimental Forest, and surveyed on a 4 m × 4 m grid. Every grid node was sampled for soil (0–10, 10–35, 35–60 cm depths) in the intact forest at the start of the experiment. All trees >10 cm diameter at breast height were measured for basal area, height, and identified to species. In June of 1989, the two treatment plots were clear cut; all aboveground vegetation was weighed and hand-carried off the plots. Trees were measured for allometric equations and subsampled for carbon and nutrient analyses [65]. Hurricane Hugo swept through the forest in September 1989, decimating the control plots. The effects of the hurricane on the treatment plots was minimal: no trees fell into the plots and the added litter was quantified and collected immediately after the storm [65]. The soils and vegetation were then intensively sampled over the next two years, and again at 10-years post-disturbance.

Clear-cutting removed 300 tons of biomass per ha and the large amount of nutrients contained therein [65]. Deforestation led to short-term increases in exchangeable cation concentrations in soils prior to the hurricane, and most soil and forest floor nutrient pools had returned to pre-disturbance levels within 9 weeks. Exchangeable potassium was the only element that declined significantly in soils over this time period. The hurricane approximately doubled the size of the forest floor pool and substantially increased forest floor concentrations of nitrogen, phosphorus, potassium, calcium and magnesium [66]. In the soil, only the concentrations of exchangeable potassium and nitrate (NO_3^-) increased significantly, but these, and the forest floor mass returned to pre-disturbance values within 9 months. Surprisingly there was no effect of the disturbances on soil organic matter content [66]. However, there was a 40% decline in live fine root biomass within 2-months of the clear-cutting, and fine root mortality increased to 70%–77% following the hurricane. Slow fine root decay led to up to 65% mass remaining after one year. Root mortality was associated with high soil NO_3^- concentrations [67]. Forest regrowth was slower in the clear-cut plots than in the surrounding forest 10 years following the disturbances. Fine root biomass recovered within 8-10 years, albeit stocks were more variable in the treatment plots than in the surrounding forest. Soil carbon stocks did not change significantly as a result of the disturbances. Soil phosphorus pools declined during periods of rapid plant regrowth, and then fluctuated over time. Overall, soil carbon and nutrient pools were relatively resilient to disturbance in this forest on a decadal time scale [68]. Deforestation is a continuing problem in tropical regions, resulting in the conversion of 97 million ha of forested land globally from 2001–2012 and the emissions of 47 Gt CO_2 [69]. Research that explores carbon and nutrient cycling in secondary forests continues to be a research need, the results of which would provide invaluable insight into the role that these forests will play in mediating future climate.

2.6. Post-Hurricane Fertilization and Debris-Removal Experiment (1989)

Hurricanes are an important force structuring Puerto Rico's forests, and have been responsible for billions of dollars in damages to U.S. coastal regions and interests [70]. Although much knowledge has been gained about forest responses to hurricanes from observational studies, a mechanistic understanding requires experimental manipulations [71]. In 1989, scientists had just finished their initial set up for a complete fertilization experiment in the Luquillo Experimental Forest when Hurricane Hugo hit Puerto Rico. They took note of the large deposits of green foliage on the forest floor, which was equivalent to over a year's worth of phosphorus being deposited in a 24-h period. In response, scientists added a debris-removal treatment to the experiment resulting in 4 blocks with 3 treatments: fertilization, control, and debris removal (1 month after Hugo). Plots were each 20 m $\times$ 20 m and scientists investigated a wide range of responses including nutrient immobilization [72], litterfall rates, quality and decay [73], earthworm responses [74], effects on understory plants [75]), as well as effects on forest growth and species composition [76]. The fertilization experiment was established in lower- (350–500 m asl) and upper-elevation forests (1050 m asl), where plots had been fertilized with macro-and micronutrients every 3 months since the passage of Hurricane Hugo in 1989 [72,76].

Fertilization stimulated leaf litter production in both forests, but the rate of recovery to pre-hurricane levels was greater at 350–500 m above sea level (20 months after treatment) than those at 1050 m asl (38 months, [64]). Litterfall increased after fertilization and by 2–3 years appeared to reach its maximum [76], with some decreases in magnitude seen a decade later [73]. Experimental removal of litter and woody debris generated by the hurricane (plus any standing stocks present before the hurricane) increased soil nitrogen availability and above-ground productivity by as much as 40% compared to un-manipulated control plots [72]. These increases were similar to those created by quarterly fertilization with inorganic nutrients. Approximately 85% of hurricane-generated debris was woody debris greater than 5 cm diameter. Thus, it appeared that woody debris stimulated nutrient immobilization, resulting in depression of soil nitrogen availability and productivity in control plots [72]. These results together with simulations of an ecosystem model (CENTURY) calibrated for Luquillo Experimental Forest [77] indicated the large wood component of hurricane-generated debris was of sufficiently low quality and of great enough mass to cause the observed effects on productivity. Scientists found no effect of fertilization on the abundance and biomass of earthworms in the upper elevation plots [74]. In the lower-elevation plots, however, the density and biomass of earthworms were significantly greater in the control than in the fertilization treatments. Surprisingly, the removal of hurricane-generated debris significantly increased the density of earthworms. Possible reasons for this positive increase maybe due to increased nitrogen availability in the litter removal soils [72], less leaching of organic compounds from coarse wood [78], and consequently, increased soil pH, and reduction of litter fauna (e.g., frogs, lizards and ants) that function as both competitors for resources and predators [74].

2.7. Canopy Trimming Experiment (2002-Today)

One of the major effects of hurricanes on forests is the defoliation and stem loss of the vegetation resulting in large openings in the canopy and significant deposition of green plant material and coarse woody debris to the forest floor. In an effort to separate the effects of canopy opening and increased debris deposition due to hurricanes, the canopy trimming experiment (CTE) was established in 2002. Canopy branches of 576 trees were trimmed and 32,448 kg of dry mass was distributed over six 30 m × 30 m plots, which is similar to what was observed after Hurricane Hugo. The experiment comprised 3 blocks of 4 full factorial treatments: no trimming and no debris added, trimming performed and debris added, trimming performed and no debris added, no trimming and debris added. Measurements for this experiment are ongoing, and a second canopy trim was conducted in 2014.

Studies within the CTE are diverse, exploring the mechanistic response patterns of tropical forest biota (microbes, plants, animals) and processes (decomposition, herbivory, nutrient cycling, primary production) to canopy and understory disturbance [27,71,79]. As a whole, results from the CTE suggest that cascading effects from canopy openness account for most of the shifts in the forest biota and biotic processes, such as increased plant recruitment and richness, as well as the decreased abundance and diversity of several animal groups [71]. Canopy opening decreased litterfall and litter moisture [80], thereby inhibiting lignin-degrading fungi, which slowed decomposition [79,81]. Debris addition temporarily increased tree basal area [49]. Data also suggest that hurricane disturbance can accelerate the cycling of soil labile organic carbon on a short temporal scale of less than two years [82]. In addition, scientists found that both surface- (0–10 cm) and subsoils (50–80 cm) have the potential to significantly increase carbon and nutrient storage a decade after the sudden deposition of disturbance-related organic debris, suggesting Luquillo Experimental Forest soils can serve as sinks of carbon and nutrients derived from disturbance-induced pulses of organic matter [83].

2.8. Long-Term Nitrogen Addition in Two Forest Types (2002–Today)

Deposition of nitrogen in tropical forests is projected to increase [84] and we know increased anthropogenic nitrogen inputs can have dramatic effects on the structure and function of plant and animal communities [85]. To understand the consequences of increased nitrogen inputs, scientists have been continually applying 50 kg per ha per year of nitrogen fertilizer to twelve 20 m × 20 m plots in two forest types within the Luquillo Experimental Forest (3 fertilized, 3 control per site) since 2002 [30]. Nitrogen additions suppressed nitrogen fixation at both high and low elevation sites [30,86] Thus far, there have been no significant effects of nitrogen fertilization on plant growth, suggesting that plants in this forest are not nitrogen limited. In contrast, significant belowground responses to nitrogen addition included increased soil carbon dioxide fluxes, decline in live root biomass, and an increase in total soil carbon. However, labile soil carbon decreased while mineral-associated carbon increased [30,86]. This work suggests that soil carbon storage may be sensitive to nitrogen deposition even in forests that are not nitrogen limited [30]. Because these plots are some of only a handful of fertilization plots in the tropics, they offer an important opportunity for understanding how changes to nutrient inputs can affect how tropical forests work.

2.9. Throughfall Exclusion Experiment (2008-Today)

In an effort to understand the consequences of drought on the biogeochemistry of tropical soils, small shelters (1.24 × 1.24 m) were installed in the forest understory of the Luquillo Experimental Forest in 2008 to divert water away from soils, effectively reducing soil moisture (Figure 5). Effects on soil gas fluxes, nutrient cycling, and microbial dynamics were studied. Soil carbon dioxide emissions declined and net methane consumption, as well as net nitrous oxide sink behavior, increased in response to reduced soil moisture. Taken together these data suggested drought may decrease greenhouse gas emissions from tropical soils [31,87]. However, microbes showed the capacity to adapt to repeat cycles of drought [32]. Following up on these initial experiments, a new throughfall exclusion experiment was established in 2017 with larger throughfall exclusion shelters (2.4 m × 4.8 m) to further explore the consequences of repeated drought on a range of biogeochemical processes. Shelters were in place for a total of 6 months when Hurricanes Irma and Maria passed over the island of Puerto Rico in September 2017. The shelters were removed during the storms, but following the hurricanes, shelters were re-established and the study was modified to include interactions between soil drought and the recovery of soil biogeochemical responses following hurricane disturbance. Results from this experiment will provide a better understanding of the interactions between droughts and hurricanes, two major drivers of environmental change at the Luquillo Experimental Forest that are projected to increase in frequency under future climate regimes.

Figure 5. Throughfall exclusion shelter installed in the Luquillo Experimental Forest. Photograph by Tana E. Wood.

2.10. TRACE: Tropical Responses to Altered Climate Experiment (2013-Today)

Temperatures are expected to increase significantly in tropical regions over the next two decades [88,89]. How already-warm tropical forests will respond to increasing temperatures remains a critical unknown in our global understanding of climate change effects. For example, whether tropical forests will continue to serve as net sinks for carbon in a warmer world remains highly uncertain [90,91]. In an effort to quantify the effects of increased temperature on tropical forest carbon cycling, scientists established the first field warming experiment in a tropical forested ecosystem in the Luquillo Experimental Forest (Tropical Responses to Altered Climate Experiment (TRACE)) [10]. In 2016, infra-red heaters were deployed in 4-m diameter hexagonal plots to warm understory vegetation and soils by +4 °C above ambient (Figure 6). Pre-treatment measurements were collected for 1-year before warming began in the fall of 2017 [10]. As with Odum's radiation experiment, scientists have taken the opportunity to explore many facets of tropical forest responses to warming, including soil carbon and nutrient fluxes and pools, plant physiology, plant demography, soil microbial communities, and responses of soil microarthropods and native frogs. In 2017, one year following the initiation of warming Hurricanes Irma and Maria passed over the island of Puerto Rico. Warming efforts were paused and scientists capitalized on the opportunity to evaluate whether the prior stress of warming influenced the recovery of forest biomass and processes following hurricane disturbance. New baseline measurements were collected for a full year following the hurricanes and warming was restarted in the fall of 2018. This unique infrastructure offers a potentially once-in-a-lifetime opportunity to assess how warmer tropical plants and soils recover from hurricanes. Experimental research at the TRACE site is ongoing, and publications on the results from the first year of warming are in progress.

Figure 6. Arial photograph of one of the TRACE plots in 2018, 14 months after Hurricane Maria. Photograph by Maxwell Farrington.

3. Conclusions

The Luquillo Experimental Forest has served as a platform for a wealth of innovative and revolutionary experiments, from the Radiation and Giant Plastic Cylinder Experiments initiated in the 1960's to the Canopy Trimming and Tropical Responses to Altered Climate Experiments established in the 2000's. To our knowledge, no other tropical forest has experienced such a range of unique experimentation, or has so clearly marked the history of the fears and interests of our society. While the responses and rates of recovery to these disturbances have been varied, the Luquillo Experimental Forest has demonstrated incredible resistance and recovery in the face of great change. Whether these forests will continue to prevail or if we will see a significant shift in the size and composition of the

Luquillo Experimental Forest as the world's climate and disturbance regimes continue to change is one of the greatest concerns facing scientists today. Current and future experiments conducted in the Luquillo Experimental Forest will continue to address these questions and will provide critical information for the development and refinement of forest management strategies.

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