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Forest recovery in abandoned tropical pastures in Puerto Rico

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Abstract

The conversion of tropical forests into pastures has increased dramatically in the last 20 years. Once these lands are abandoned it is not clear if they will recover to forest or if they will become permanent grasslands. Economic changes in Puerto Rico have led to the abandonment of agricultural lands over the last 60 years, providing an opportunity to assess the longer term patterns of forest recovery following human disturbance. This study focuses on the changes in vegetation in abandoned pastures ranging in age from 0 to 60 years or more in two replicate chronosequences. Species richness and density of woody species were very low during the first 10 years following abandonment and woody biomass did not increase substantially until approximately 15 years post-abandonment. Recovery in pastures is greatly delayed in comparison with forest recovery following other types of human and natural disturbance. The successional trajectory is quite different in comparison to those following natural disturbances in the nearby Luquillo Mountains. In particular, the initial colonizing species are not 'typical' pioneer species (e.g. *Cecropia* sp., *Scheffleria morotoni*), but a group of shrubs and treelets in the Rubiaceae, Melastomataceae, and Myrtaceae. The presence of grasses and the rapid colonization and growth of ferns and herbaceous species in the abandoned pastures appears to be a major factor inhibiting the establishment of secondary forest and imparts a selective barrier on the colonizing woody species.

Keywords: Forest structure; Land use history; Secondary succession; Tropics; Pasture; Abandonment

1. Introduction

Throughout the tropics, extensive areas of forested ecosystems have been converted into pastures (World Resources Institute, 1992). These pastures are rarely active for more than 10 years and, in many cases, they are abandoned much sooner because of soil degradation, invasion of unpalatable grasses, or

changing economic incentives (Buschbacher, 1986; Serrão and Toledo, 1990; Hecht, 1993). As tropical deforestation continues, a greater proportion of land area will become anthropogenic grasslands and secondary forest (Brown and Lugo, 1990; Finegan, 1992). While preserving primary forests is the preferred method for maintaining tropical diversity, the conversion of abandoned pastures into secondary forest can greatly contribute to the maintenance of biodiversity. A sound understanding of the vegeta-

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tion dynamics and the factors that control these dynamics is needed to effectively manage or restore secondary forest in abandoned pastures.

The Caribbean island of Puerto Rico is one of the few tropical sites in the world where reforestation is occurring at a higher rate than deforestation (Birdsey and Weaver, 1987). Economic changes that occurred after World War II have dramatically decreased the pressure of human activities on local forests. During the 1940s, the governments of Puerto Rico and United States promoted a major shift in the economic base of the island from agriculture to industry (Dietz, 1986). This led to the abandonment of agricultural lands across the island and the extensive recovery of secondary forest (Birdsey and Weaver, 1987). During the last 40–50 years, forest cover has increased from approximately 5% to over 30% (Birdsey and Weaver, 1987). Ecological studies that focus on the process of forest recovery can help build models for designing management and restoration projects in other tropical areas.

In this study we focus on the patterns of forest

recovery in abandoned pastures. Previous studies in tropical (Buschbacher et al., 1984) and temperate sites (Myser and Pickett, 1990) suggest that recovery will be much slower in abandoned pastures in comparison with regeneration following natural disturbances (e.g. treefalls and hurricanes) because of the inhibition of tree establishment. Some of the factors that may contribute to the prolonged recovery of pastures are: lack of forest tree propagules, high levels of seed and seedling predation, degraded soils, or competition with established grasses and herbaceous species (Nepstad et al., 1990; Aide and Cavellier, 1994). We document the change in the species richness, species composition, and the structural diversity of the plant community of abandoned pastures of different ages. These data are compared with studies of regeneration: in the neighboring Luquillo Mountains (e.g. Crow, 1980; Weaver, 1990); following slash and burn agriculture (Uhl, 1987; Brown and Lugo, 1990); in abandoned pastures in the Amazon (Uhl et al., 1988), and in plantations in Puerto Rico (Lugo, 1992; Parrotta, 1992).

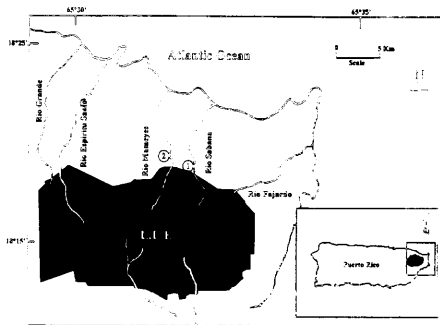


Fig. 1. Map of northeastern Puerto Rico, the Luquillo Experimental forest (LEF), and the locations of study sites along the (1) Rio Sabana and (2) Rio Mameyes.

2. Methods

The study was conducted in abandoned pastures within the Rio Sabana and Rio Mameyes watershed to the north of the Luquillo Experimental Forest (LEF) in north-eastern Puerto Rico (Fig. 1). The vegetation is subtropical wet forest and areas which have received little human disturbance are dominated by *Dacryodes excelsa* (Burseraceae), *Manilkara bidentata* (Sapotaceae), and *Sloanea berteriana* (Elaeocarpaceae) (Ewel and Whitmore, 1973). There is little seasonal variation in rainfall (Bisley experimental watershed averages approximately 3000 mm year⁻¹; Scatena, 1989) or temperature (mean annual 25°C; Brown et al., 1983). Hurricanes are an important source of natural disturbance in Puerto Rico and the most recent hurricane, Hugo (September 1989), caused extensive damage to the LEF (Walker et al., 1991).

2.1. Land use history

In the lower elevations of the Luquillo Mountains, land use practices have been diverse and on a small scale (0.1-10 ha) (Scatena, 1989; García-Montiel and Scatena, 1994). The area was colonized during the 1800s and the forest was converted to pastures, coffee plantations, or used for cultivation of subsistence crops. Successive hurricanes in 1899, 1928, and 1932 caused severe damage to coffee plantations which led to the decline of this industry throughout the island (Dietz, 1986). In the Luquillo Mountains, these hurricanes forced many people to abandon agricultural lands and most of these lands were eventually purchased by the USDA Forest Service during the 1930s and 1940s (Brown et al., 1983). Along the current boundary of the LEF, local people continue to raise small herds of cattle and farm small areas.

2.2. Study sites

Aerial photographs taken in 1936, 1951, 1964, 1971, 1977, 1983, 1988, 1991, and 1993 were used to initially select sites. Land owners were contacted for more detailed information on land use history. Six sites were selected along both the Rio Sabana and Rio Mameyes (Fig. 1, Table 1). Five sites were

Table 1

Characteristics of the study sites. The size, the length of time that each area was in pasture and the range of age of abandonment were estimated from aerial photographs. The estimated ages (approximate mid point of the range) correspond to 1993 when the vegetation was sampled

Site	Size (ha)	Time cleared (years)	Range of age abandoned pasture (years)	Estimated age (years)
<i>Sabana</i>				
1	4.0	> 40	0	0
2	10.0	> 40	5-10	7
3	1.0	15-20	10-15	12
4	7.0	15-20	20-25	22
5	11.0	15-20	22-29	25
6	16.0	0	≥ 60	60
<i>Mameyes</i>				
1	6.8	> 50	0	0
2	2.5	> 50	5-10	7
3	6.0	10-15	20-25	22
4	2.5	30-35	22-29	25
5	5.0	20-25	29-42	35
6	54.0	0	≥ 60	60

pastures (Sabana, 0 to about 25 years since abandonment; Mameyes, 0 to about 35 years since abandonment) and one site was forested for at least the last 60 years. The forested sites had forest cover in the 1936 photograph, no evidence of intervention in more recent photographs, and are considered to represent 'mature' forest. The time since abandonment was estimated by taking the mid point between the last photograph to show pastures and the next photograph that showed signs of abandonment (e.g. tall grasses, shrubs, or trees). All sites were located within 1 km of the LEF northern boundary and ranged in size from 1.0 to 54 ha (median 4.8 ha). The sites are on slightly to moderately steep slopes between 100 and 150 m elevation. Soils ranged from silty clay loams to clays (Boccheciamp, 1977) and were primarily Ultisols in the Humatas series (Rio Mameyes) and Zarzal-Cristal complex (Rio Sabana; Johnston, 1992).

2.3. Vegetation analysis

The size and shape of the abandoned pastures were very different. To minimize edge effects we sampled the middle of each site. The vegetation of

each site was described along three 45 m transects. Transects were laid at 15 m intervals perpendicular to the slope. The vegetation was sampled every 5 m along the transect in ten 1 m × 1 m quadrats. Percent cover of non-woody vegetation (herbaceous vegetation, ferns, grasses) was estimated in each quadrat. All woody plants 1 cm or over in diameter at breast height (dbh, 1.3 m) were identified and their height and diameter were measured. With the exception of two 0-year-old and two 7-year-old sites which had no or few woody species, species area curves of woody species did not approach an asymptote with this sampling scheme. In the eight sites greater than 7 years old, all woody species of at least 1 cm dbh were identified, and diameter and height were measured in an additional 1 m × 45 m transect situated between the first and second transect. The inclusion of the information from the fourth transect caused all species area curves to approach an asymptote. Im-

portance values for the woody vegetation were calculated as the mean of relative frequency and basal area.

Biomass of non-woody vegetation was estimated in one randomly chosen quadrat per transect (three per site). The vegetation was collected, separated by species, dried at 70°C, and weighed. The above-ground biomass for woody vegetation greater than 1 cm dbh was estimated using all individuals in the four transects and the equations of Weaver and Gillespie (1992). Nomenclature follows Little and Wadsworth (1964) and Little et al. (1974).

3. Results

3.1. Non-woody vegetation

The biomass and percent cover of non-woody vegetation increased after abandonment to a peak in

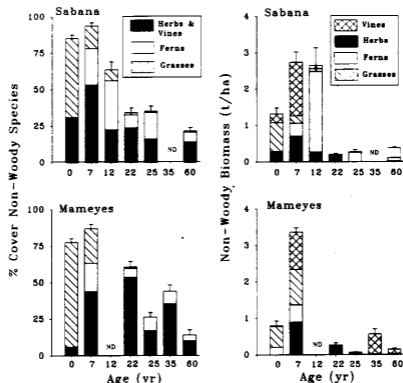


Fig. 2. Relationship between age since abandonment and non-woody species percent cover and aboveground biomass. The standard error bar represents the variation in total plant cover ($n = 30$ per site) and total non-woody biomass ($n = 3$ per site). No 12-year-old sites in Mameyes or 35-year-old sites in the Rio Sabana were available for sampling. ND, no data.

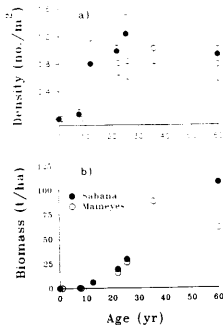


Fig. 3. Relationship between age since abandonment and (a) mean (\pm SE) density (at least 1 cm dbh) and (b) woody species above-ground biomass (at least 1 cm dbh). Woody biomass was estimated using the following equations from Weaver and Gillespie (1992): dbh less than 5 cm – biomass = $0.2847D^{1.4417}$, dbh 5 cm or over – biomass = $2.669 - 2.2832D + 0.5491D^2$, where D is diameter.

the 7-year-old sites and then declined to low levels as woody species began to produce a closed canopy (Fig. 2). The maximum non-woody biomass was measured in the two 7-year-old sites (Sabana, 2.7 t ha⁻¹; Mameyes, 3.4 t ha⁻¹). In the sites at least 60 years old, non-woody biomass dropped to less than 0.1 t ha⁻¹. The active pastures were dominated by grass (*Axonopus compressus*), but once abandoned, herbs (e.g. *Commelina* sp., *Desmodium adscendens*, *Clidemia hirta*), vines (e.g. *Ipomea* spp.), and ferns (e.g. *Nephrolepis* sp., *Thelypteris deltoidea*) became important components.

3.2. Woody vegetation

During the first 7 years, there was virtually no woody vegetation in the abandoned pastures, but during the next 10–15 years the density increased rapidly (Fig. 3(a)). Densities were less than 0.1 trees

m⁻² in sites less than 10 years old and increased to a maximum of 1.3 trees m⁻² in the 25-year-old site. Beyond that age, tree densities remained approximately the same (Fig. 3(a)). The pattern of above-ground woody biomass accumulation lagged behind tree densities (Fig. 3(b)). During the first 12 years, woody biomass was less than 6 t ha⁻¹ and even in sites that have been abandoned for 20–25 years the woody biomass was less than 30 t ha⁻¹. The rate of biomass accumulation during the first 22 years was less than 1.0 t year⁻¹, but accumulation increased to 3.5 t year⁻¹ between the 22- and 25-year-old sites (Fig. 3). The Sabana site that was over 60 years old had the highest woody biomass (107 t ha⁻¹).

The mean plant height increased from zero to approximately 3 m during the first 10–20 years (Fig. 4). In the 20–60 year old sites the median height did not increase significantly, but there was a large increase in the range. The distributions of tree diameters in the two areas showed a similar pattern; an early increase in the median value and a consistent increase in the range with age since abandonment (Fig. 4).

In both chronosequences, there was a positive relationship between site age and woody species richness (Fig. 5). There were no or very few woody species in the young sites (under 10 years old), but

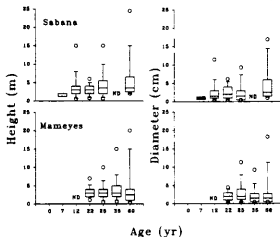


Fig. 4. Relationship between age since abandonment and the distribution of plant height and diameter of woody species in sites along the Rio Sabana and the Rio Mameyes. Box plots illustrate the median (horizontal line within the box), 25–75 percentiles (the box), 10–90 percentiles (T), and values greater than the 10–90 percentiles (O).

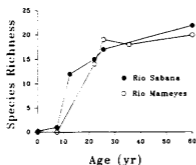


Fig. 5. Relationship between age since abandonment and woody species richness (number of species).

during the next 15 years there was a rapid accumulation of species to levels similar to that observed in the oldest sites (about 20 spp.). Although there was an increase in woody species richness, sites less than 25 years old were dominated by a single species, *Miconia prasina* (Table 2).

3.3. Successional pattern

Based on changes in the biomass of non-woody species and the importance values of woody species, the chronosequences suggest the following successional patterns. Initially, the abandoned pastures are dominated by grasses, which were then colonized by vines, herbs, and ferns (Fig. 2). Saplings of woody species (at least 1 cm dbh) first appeared in the 7-year-old site, and their densities increased over the next 10-15 years (Fig. 3, Table 2). The woody species that first colonize the pastures were mainly shrub and small tree species in the Melastomataceae (e.g. *Miconia prasina*, *Miconia impetolaris*) and Rubiaceae (e.g. *Palicourea riparia*, *Psychotria brachiata*) (Table 2). Importance values for *Miconia prasina* were greater than 50% in abandoned pastures between 12 and 25 years old (Table 2). After about 22 years, the shrub and treelet species reached their maximum densities (Fig. 3) and produced a closed canopy which lead to the dramatic decrease in

Table 2
Importance values (% density + % basal area/2) for woody species that had at least 5.0% in at least one site

Species	Family	Age since abandonment site ^a (years)								
		7 _S	12 _S	22 _S	22 _M	25 _S	25 _M	35 _M	60 _S	60 _M
<i>Miconia prasina</i>	Melastomataceae	100.0	70.3	79.6	55.9	1.1	51.6	14.0	0.7	
<i>Myrcia deflexa</i>	Myrtaceae			2.1		8.3				
<i>Miconia serrulata</i>	Melastomataceae				12.7		0.7			
<i>Tabebuia heterophylla</i>	Bignoniaceae					15.7				
<i>Miconia impetolaris</i>	Melastomataceae		11.3	0.6					1.4	2.5
<i>Psychotria brachiata</i>	Rubiaceae			5.1	2.5		12.5	13.5	4.6	2.4
<i>Palicourea riparia</i>	Rubiaceae		1.0	1.8		16.8	10.8	11.6	1.6	0.6
<i>Syzygium jambos</i>	Myrtaceae		3.4		0.8	17.7		5.9	2.8	
<i>Myrcia splendens</i>	Myrtaceae					31.0	1.8		3.3	1.3
<i>Rauwolfia nitida</i>	Apocynaceae				18.3			0.7		
<i>Andira inermis</i>	Leguminosae		8.6		3.1		9.1	10.0		35.1
<i>Guarea guidonia</i>	Meliaceae					0.5	4.9			5.9
<i>Psychotria berteriana</i>	Rubiaceae			1.3				3.1	8.9	
<i>Casearia arborea</i>	Flacourtiaceae							5.5	3.7	
<i>Prestoea montana</i>	Palmae				4.2				7.5	
<i>Piper glabrescens</i>	Piperaceae						0.7	0.7	5.8	7.5
<i>Cecropia schreberiana</i>	Moraceae						0.8	15.5	20.1	12.8
<i>Artocarpus altilis</i>	Moraceae							12.5		
<i>Ficus citrifolia</i>	Moraceae								28.3	
<i>Ochroma pyramidale</i>	Bombacaceae									9.0
Total		100.0	94.6	90.5	97.5	91.1	92.9	93.0	88.7	77.1

^a Subscript indicates site: S, Sabana; M, Mameyes.

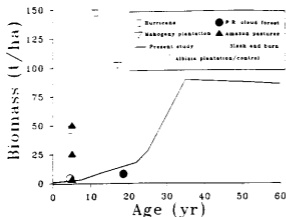


Fig. 6. Comparison of aboveground biomass estimates for the Puerto Rican pasture chronosequence (solid line) and various other studies of forest recovery. Recovery following Hurricane San Ciprian (1932) in tabonuco forest in Puerto Rico (\square) (Crow, 1980). ∇ , a *Swietenia macrophylla* plantation in the area of the Sabana pasture sites (Lugo, 1992); \circ , *Albizia lebbek* plantations (higher value) and control site in coastal pastures in Puerto Rico (Parrotta, 1992); \bullet , recovery of cloud forest following denudation from a plane crash (Weaver, 1990); \blacktriangle , recovery of abandoned pastures that received light, intermediate, and heavy use (Uhl et al., 1988). The dotted line represents the rate of recovery following slash and burn agriculture (from Uhl, 1987, fig. 8; Brown and Lugo, 1992, fig. 3).

the herbaceous understory vegetation. Forest pioneer species, *Cecropia schreberiana* (Moraceae), *Ochroma pyramidale* (Bombacaceae) and *Schefflera morototoni* (Araliaceae), were not important colonizers of the abandoned pastures and occurred only in the older sites. *Cecropia schreberiana* and *Andira inermis* had the highest importance values in the oldest sites (Table 2).

4. Discussion

Forest recovery is slower in the abandoned pastures along the Rio Sabana and Rio Mameyes in comparison with recovery following other natural and human disturbances in the tropics (Fig. 6). We observed little or no aboveground woody biomass in the 15-year-old abandoned pastures and woody biomass was only about 100 t ha^{-1} after 35 years (Figs. 3(b) and 6). In comparison, 11 years after Hurricane San Ciprian (1932) passed over tabonuco

forest in El Verde, Puerto Rico (350 m), the aboveground woody biomass had recovered to 147 t ha^{-1} (trees over 4 cm dbh) (Crow, 1980) (Fig. 6). A 17-year-old *Swietenia macrophylla* plantation in the Rio Sabana watershed of the Luquillo Mountains (Lugo, 1992) had approximately 10 times greater woody biomass than that predicted by the chronosequence of the abandoned pastures (Fig. 6). The woody biomass of a 4.5-year-old *Albizia lebbek* plantation established in coastal pastures in Puerto Rico was 46 t ha^{-1} (Parrotta, 1992) compared with 4.2 t ha^{-1} in unmanipulated coastal pastures (control sites). During this experiment, 11 additional woody species colonized the plantations and no woody species colonized the control plots (Parrotta, 1992). Aboveground woody biomass in a cloud forest, 18.5 years following an airplane crash which denuded the vegetation (Weaver, 1990), was only slightly lower than what we observed in the abandoned pastures (Fig. 6). Normal annual biomass accumulation in cloud forest is 5.5 times less than in the wet forest vegetation zone where the pastures occur (Weaver and Murphy, 1990). Compared with other areas and land uses in Puerto Rico, recovery in pastures is most similar to cloud forest, the least productive habitat.

Reviews of forest recovery following slash and burn agriculture (Uhl, 1987) or shifting agriculture (Brown and Lugo, 1990) estimate the rate of forest biomass recovery to be $5 \text{ t ha}^{-1} \text{ year}^{-1}$, a value much greater than we observed (Fig. 6). In a separate study, Uhl et al. (1988) showed that recovery in Amazon pastures varied depending on the intensity of use. Pastures that received intermediate levels of use recovered at approximately the same rate as areas that were used for slash and burn agriculture. The slowest rates of recovery were in areas of heavy use, where bulldozers were used to remove trees and to prepare the site. Rates of recovery in these highly disturbed sites were most similar to the patterns observed in our study. Although there are many factors that could inhibit recovery in the abandoned pastures, the initial barrier will be a lack of propagules. Forest regeneration may occur by four pathways: (1) advance regeneration (seedlings); (2) sprouts; (3) seed bank; (4) seed dispersal (Uhl et al. 1990). Given that our sites were in use for at least 1 year and as much as 30–40 years (Table 1), the

major pathway for regeneration will be from seeds dispersing into the sites. Seedlings, sprouts, and the seed bank from the original forest stand would have been eliminated after a couple of years of continuous use (Uhl et al., 1990). Our sites are small in comparison with pastures in other tropical regions, but given that seed dispersal can be limited to within 10 m from the forest edge (Aide and Cavalier, 1994), seeds still could be a major limitation. When other pathways of regeneration are available recovery is faster. Although hurricanes cause extensive damage, recovery can occur from sprouting, seedlings, or the seed bank. Similarly, because the duration of slash and burn agriculture is usually only a few years, seedlings, sprouts, and the seed bank can still contribute to the recovery process. These sources of regeneration are not available in pastures.

Even when tree seeds disperse into the abandoned pastures the thick vegetation may prevent tree seeds from reaching the soil and seeds that do germinate must compete with the established herbaceous vegetation. Parrotta (1992) bypassed the dispersal barrier by planting seedlings of *A. lebbek* and reduced the competitive affect by weeding. This treatment dramatically increased the biomass accumulation of *A. lebbek* and also allowed the establishment of many other tree species.

The prolonged use of our pastures and the degradation of the soils is another factor that could delay forest recovery (Reiners et al., 1994). The soil characteristics of these sites are presently being studied and preliminary results have shown that the soils in the younger sites have high compaction and have lost soil structure (D. García-Montiel, personal communications, 1995). These conditions result in poor infiltration, greater runoff, and increased erosion. Although the condition of the soils may be an important barrier, the degradation of pasture soils can be much greater in regions where fire is frequently used (Aide and Cavalier, 1994).

Forest recovery in these abandoned pastures is slow, but the successional process has not been arrested. In other tropical regions, the use of fire is an important factor that acts to maintain anthropogenic grasslands in Colombia (Aide and Cavalier, 1994) and Brazil (Uhl and Buschbacher, 1985). The lack of reforestation in these sites has caused the continued degradation of the soils and promoted the

savannization of these areas (J. Cavalier et al., unpublished data, 1995). In our study sites, the lack of fire, the small size of the pastures, and the nearby intact forest are factors that should contribute to rapid recovery. In comparison with Finegan's (1992) model of neotropical secondary succession, the slower recovery in our sites is most likely due to the dominance of herbaceous biomass during the first 10 years.

In Ghana (Swaine and Hall, 1983), Mexico (Purata, 1986), Venezuela and Brazil (Uhl et al., 1990), woody vegetation recovered quickly (1–5 years) following forest clearing and the colonizing species (e.g. *Macaranga* in Ghana, *Cecropia* in Mexico, Venezuela and Brazil) were similar to those found in natural disturbances in the nearby forest. *Cecropia schreberiana* is the dominant pioneer species following treefalls, hurricanes, and landslide in the LEF (Crow, 1980; DeVoe, 1989; Guariguata, 1990), but it appears to be unable to establish in the abandoned pastures (Zimmerman et al., 1995). The first woody species to colonize the abandoned pastures were shrubs and treelets in the Melastomataceae, Myrtaceae and Rubiaceae families. Kellman (1985) has experimentally shown that the presence of shrubs is critical for the establishment of tree species in savannas. These observations suggest that certain shrub and treelet species have germination and growth characteristics that allow them to compete with well-established grasses. Future restoration efforts should consider the use of shrubs species to colonize pastures, shade out grasses, and create microhabitats that will facilitate the establishment of tree species.

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