

Fire Ecology of the Guayana Region, Northeastern South America

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ABSTRACT

The summits of high sandstone mesas rising from the Guayana Shield of northeastern South America (principally in southeastern Venezuela) are vegetated by herbaceous and shrubby boglands and evergreen shrub/tree forests rooted on saturated peat soils. High annual rainfall, frequent electrical storms, and a three-month dry season characterize the relatively flat summit terrain of these mesas, called "tepui" by the Pemon Amerindians. The mesas and surrounding lowlands are collectively known as the Guayana region. Fires on tepui summits and flanks are described from personal observations made on walking expeditions to five tepuis, and from a survey of the scientific literature. Lightning-ignited fires appear to be rare on tepui summits, but anthropogenic fires are on the increase. Numerous fires on tepui flanks and in the Gran Sabana plains between tepuis are described. Increased anthropogenic fire frequency in the past two centuries has resulted in the expansion of treeless savanna at the expense of lowland and tepui flank rainforests, obscuring the natural fire ecology relationships between vegetation and lightning. Putative adaptations to survive fire found in several plant families that occur both on tepui summits and at lower elevations suggest that natural, lightning-ignited fire has played an evolutionary role in the Guayana region.

RESUMEN

Las cumbres de mesas altas de arenisca que se levantan desde el Escudo Guayanés en la parte noreste de Sudamérica (principalmente en la región sureste de Venezuela) tienen vegetación pantanal y herbácea con arbustos, y tienen bosques perennes de arbustos y árboles. Estas mesas se llaman "tepuyes", y esta palabra pertenece al idioma de los Amerindios Pemón. Mucha lluvia al año, tormentas eléctricas frecuentes, y una época seca que dura tres meses caracterizan las cumbres casi planas de los tepuyes. Las cumbres y sus bajos alrededores son en grupo conocidos como la región de la Guayana. Se describen los fuegos que arden al lado y en las cumbres de los tepuyes por medio de observaciones personales de expediciones a pie a cinco tepuyes distintos, y de investigación de la literatura científica. Los fuegos incendiados por relámpago en las cumbres de tepuyes no parecen ser muy frecuentes, pero los fuegos antropogénicos están aumentando. Se describen muchos fuegos antropogénicos que arden al lado de los tepuyes y en la plana Gran Sabana entre los tepuyes. La frecuencia de fuegos antropogénicos ha aumentado durante los últimos dos siglos. Debido a este hecho, las selvas entre y alrededor de los tepuyes se han reducido, y la sabana (sin árboles) se ha extendido. Hay varias familias de plantas que viven en las cumbres y en los planos alrededores de los tepuyes que se supone se adaptan para sobrevivir los fuegos. Esto sugiere que el fuego natural encendido por relámpago ha tomado parte en la evolución de las cumbres de tepuyes y, al mismo tiempo, en las elevaciones más bajas en la región de la Guayana.

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INTRODUCTION

Only 27 of 376 (7%) fire ecology research papers published in the first 18 proceedings of the Tall Timbers Fire Ecology Conferences have dealt with fire in the tropical regions of the world (between about 25°S and 25°N latitude), and only 4 have specifically dealt with South America (Fischer 1980). South America contains

immense landscapes in which naturally and human-ignited fires are common—paramo, savanna, and pampa—to name but a few.

East of the Andes and north of the Amazon River lies the Guayana Highlands (Figure 1), a vast natural area (> 200,000 km²) of vertical walled mesas rising from tropical rainforest. The mesas, called *tepui* (tepui, sin-

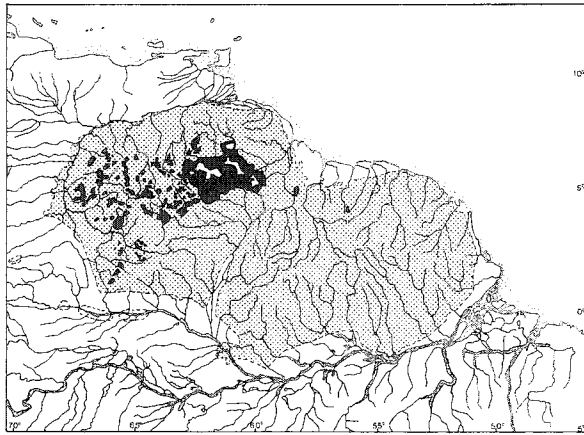


Fig. 1. Map of the Guayana Shield (stippled area) and of the Roraima Formation (black). The white areas in the Roraima Formation represent gabbro (after Bisschops 1969; Gansser 1954; Priem, et al. 1973). The Guayana Highlands consist of all the Roraima Formation. The Guayana region includes all of the Guayana Shield and the Guayana Highlands.

gular) in the Pemón language of the Carib linguistic stock, lie on top of the Guayana Shield (Figure 1), one of the two oldest landmasses of South America (Gansser 1954). Together with the Brazilian Shield south of the Amazon River, the two shields represent part of the ancient continent of Gondwana (Steyermark 1986). The Guayana Shield forms a basement of igneous and metamorphic rocks consisting of highly crystalline granites, porphyries, gneisses, and shists of Proterozoic age (Gansser 1954; Gibbs and Barron 1983).

The Guayana Highlands and Guayana Shield together make up the Guayana region. Geographically, the Guayana region lies principally in southeastern Venezuela and includes the countries of Guyana, Suriname, French Guiana, northern Brazil, and outliers in Colombia.

Venezuelan ecologists have subdivided the Guayana region into three altitudinal levels (O. Huber, pers. comm.), as follows: a) Lowlands, 0–500 m above sea level (e.g., Esmeralda savannas, vicinity of Kamarata, vicinity of Canaima); b) Uplands, ca. 500–1500 m (e.g., Gran Sabana, Guaiquinima, Parima); c) Highlands, ca. 1500–3000 m (e.g. tepui summits). For the purposes of this paper, I substitute Midlands for the term Uplands because the latter has a specific ecological meaning. This paper focuses on the fire ecology of the tepuis of the Guayana region in southeastern Venezuela.

Tepuis are erosional remnants of the Precambrian Roraima Formation, a series of well-bedded quartz sandstones that had accumulated to depths of about 3,000 m on top of the Guayana Shield (Priem et al. 1973; Ghosh 1977). Four-fifths of the original approximately

1,000,000 km² of the Roraima sandstones have been removed by erosion, leaving a topography that is pimply with scattered, and isolated, tepuis (Gansser 1974). K-Ar measurements on basalt intrusions into the Roraima Formation indicate that the sandstone beds were deposited about 1.6 billion years ago (Priem et al. 1973). Their distinct sedimentary characteristics (cross-bedding, ripple marks, slumping, etc.) suggest an origin as stream and delta deposits laid down in continental to epicontinental environments (Priem et al. 1973).

The sandstone tepuis which form the Guayana Highlands, also called Pantepui (Mayr and Phelps 1967), principally occur in the western half of the Guayana Shield in the states of Amazonas and Bolivar of southeastern Venezuela (Figure 2). Tepuis rise in elevation to slightly over 3,000 m (Table 1). Cerro Neblina on the Venezuela/Brazil border has the distinction of being the highest point on the South American continent east of the Andes. Tepuis in Estado Bolivar rise from La Gran Sabana, an elevated plain roughly 700 to 1400 m in elevation (Mayr and Phelps 1967; Maguire 1970; Steyermark 1982). Tepuis close to the Orinoco River in Estado Amazonas rise from tropical lowlands of only a few hundred meters in elevation. Tepuis in Estado Amazonas, therefore, usually have a greater base-to-peak height, and concomitantly, a greater transect of ecological zones along their slopes.

The highly variable summit areas of tepuis range from small towerlike peaks less than 1.0 km² such as Autana, Upuigma, Wadacapiapue, and Tramen to gigantic massifs such as Auyán (≈700 km²), Duida (≈1,100 km²), Chimantá, Jaua-Sarisariñama, Guaiquinima, and Neblina. Characteristically, tepui sandstone erodes in straight-sided blocks so that the relatively flat tepui summits are flanked on all or most sides by one to three tiers of vertical cliffs, 100–1000 m high. The fallen blocks lie jumbled in forested talus slopes at the bases of the cliffs (Figure 3).

Roraima Formation sandstone beds have not been appreciably deformed structurally in eastern Venezuela, but westward into Estado Amazonas the larger sandstone mountains of Duida, Cuao-Sipapo, Parú, and Neblina display faulted and folded beds. The interior of the larger Amazonas tepuis is often depressed so that the exterior margins of the tepui summit form the interfluges of a large drainage basin which flows inward into a large canyon that exits the tepui on one side (e.g. Duida, Neblina, Auyán, Parú, etc.).

Tepuis of Estado Amazonas, located close to the master stream of the region, the Orinoco River, are separated by vast reaches of tropical lowland rainforest growing on thin soils developed from the crystalline rocks of the Precambrian basement. Tepuis of Estado Bolivar,



Fig. 2. Prominent tepuis of the Guayana Highlands in Estado Bolivar and Estado Amazonas of southeastern Venezuela.

for the most part, rise from deep sands and clays weathered out of the Roraima sandstone beds. Most of the land between the tepuis of Estado Bolivar is also heavily forested, but large parts of La Gran Sabana, lying between Auyantepui and Mt. Roraima, is treeless except for gallery forests.

The climate of the Guayana region in Venezuela is reasonably uniform from one part to another, with annual rainfall in excess of 2,000 mm throughout the region, and greater than 3,000 mm on tepui summits (MARNR 1985). Most of the rainfall is distributed from March to November. A "dry" season commences in December and reaches the lowest rainfall in January and February (MARNR 1985). Winds are prevailing out of the east to southeast in Estado Bolivar to no prevailing direction in the northeastern part of Estado Amazonas (MARNR 1985). Mean annual temperatures range from $>26^{\circ}\text{C}$ in the lowland rainforests adjacent to the major rivers draining the Guayana Highlands to $<15^{\circ}\text{C}$ on tepui summits (MARNR 1985).

Study of the vegetation of tepui summits has progressed in two phases (Huber 1990). The first was the period of large expeditions on foot which began in 1884 with the ascent of Mt. Roraima by a British expedition led by Everard Im Thurn (Im Thurn and Oliver 1887). Cerro Duida was next ascended and explored in 1928–29 by the Sydney F. Tyler expedition of the American Museum of Natural History (Tate and Hitchcock 1930; Gleason 1931). W. H. Phelps organized the first scientific expedition to the summit of Auyantepui in 1937–38 (Tate 1938; Gleason and Killip 1939).

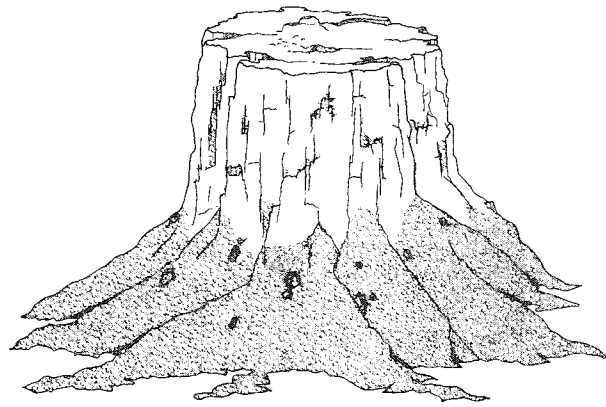


Fig. 3. Generalized silhouette of a small tepui with vertical cliffs fringing the summit, and cliff breakdown scree on talus slopes.

The second, modern, phase of tepui exploration, dating from the 1940s to the present, was characterized by a systematic exploration of Pantepui and its highlands with increasing reliance on helicopter transportation to the tepui summits. Literature and history of botanical exploration of tepuis is thoroughly reviewed in Huber and Wurdack (1984) and Huber (1990). Weibezahn and Janssen-Weibezahn (1990) have compiled an invaluable bibliography of all the literature on Estado Amazonas.

From 1987–1993 I traveled on foot and by boat throughout the Guayana region in Venezuela on 14 separate trips over a total of 10 months. The purpose of these trips was to familiarize myself with the geology, geography, and ecology of the region and to gather information for a book about the natural history of tepuis and the Guayana region (Means 1995). In the course of these travels I observed many fires actively burning, or the aftermath of numerous fires.

Fire is an important part of the ecology of the Guayana region, especially in the savannas at the bases of many tepuis. The origins of these fires, however, and their role in the natural ecology of tepuis, savannas, and local rainforests are poorly understood. In this paper I review the literature and report my personal observations of fires on the flanks and summits of only a few of the approximately fifty tepuis of the Guayana Highlands. It is my desire that this initial survey will stimulate others to study the fire ecology of this biologically rich, relatively undeveloped, yet vulnerable part of the world.

WETLAND PLANT COMMUNITIES OF THE GUAYANA HIGHLANDS

Because of the high annual rainfall, many, if not most, of the plant communities on tepui summits can be classed as wetland vegetation. Most definitions of

Table 1. The most prominent tepuis of the Guayana Highlands, listed in descending elevation.

Name	Elevation in m (ft) (Sources)
Neblina	3014 (9888) (1, 2); 3045 (7)
Pico 31 de Marzo	2992 (9816) (1, 2)
Roraima	2810 (9219) (1, 5, 6); 2772 (9094) (2, 3); 2900 (7)
Tramen	2800 (9186) (7)
Kukenán (=Cuquenán)	2680 (8790) (1, 6); 2700 (7)
Aprada	2652 (8699) (3); 2400 (4, 6)
Tirepon	2650 (8692) (8)
Ilu	2620 (8594) (1); 2800 (9186) (7)
Wadakapiapue	2600 (8528) (7)
Murosipan	2600 (8528) (7)
Kamarkawarai	2590 (8495) (1, 4); 2700 (8856) (7)
Ayantepui	2580 (8462) (1); 2950 (5); 2957 (2, 3); 2560 (4, 6); 2400 (7)
Marahuaka	2579 (8461) (1, 2, 4); 2890 (7)
Ptarai	2520 (8268) (9)
Sarisariñama	2500 (8200) (3)
Curutu	2499 (8199) (9)
Yaví	2441 (8009) (1); 2285 (4,6); 2441 (5); 2280 (7)
Churi	2420 (7938) (8)
Yuruani	2400 (7872) (10)
Yutajé	2400 (7872) (10)
Duida	2396 (7861) (1, 4); 2450 (7)
Uei	2370 (7776) (1, 2, 3, 6)
Abacapa	2359 (7738) (8)
Pico Tamacuari	2340 (7677) (1)
Chimantá	2320 (7610) (1, 5); 2713 (8899) (3); 2200 (7); 2698 (8)
Guanay	2300 (7546) (6, 7, 9)
Yumari (Sipapo)	2260 (7415) (2)
Acopan	2248 (7373) (8); 2713 (1); 2317 (3)
Jaua	2231 (7318) (1)
Upuigma	2225 (7298) (6)
Cuao	2200 (7216) (10)
Aparaman	2134 (7000) (2); 2400 (7)
Avispa	2112 (6929) (1)
Pico Guimaraes Rosa (border)	2108 (6914) (1, 3)
Guaiquinima	2100 (6890) (1, 4, 5); 1800 (5906) (2, 6); 2103 (7)
Tereke-Yuren	2100 (6888) (7)
Ayanganna (Guyana)	2036 (6680) (1); 2042 (6699) (2)
Paraque (=Sipapo?)	2030 (6660) (1); 2080 (6824) (2)
Parú	1999 (6558) (2); 2560 (5); 1650 (7)
Ovana (=Sipapo?)	1978 (6490) (1, 2)
Uaipan (=Guayapo?)	1950 (6396) (6)
Corobo	1904 (6247) (1)
Venamo	1890 (6201) (2, 6)
Turagua (Trueño)	1839 (6033) (1, 2)
Camani	1800 (5904) (10)
Huachamakare	1734 (5636) (4); 1700 (6); 1708 (7)
Chanaro	1672 (5486) (2)
Aracamuni	1600 (5248) (7)
Venamo	1600 (5248) (10)
Vinilla	1510 (4954) (1)
Guanacoco	1500 (4920) (10); 1350 (4428) (4)
Yapacana	1344 (4409) (1); 1250 (4); 1345 (6)
Cerbatana	1320 (4331) (2); 1320 (4)
Paurai	1250 (4100) (6)
Autana	1208 (3963) (1)
Pico Rondon (Brazil)	1189 (3901) (1)
Tafelberg (Surinam)	1080 (3542) (6)
Cerro Tacuto	1049 (3442) (1)
Cerro Delgado Chalbaud	1047 (3435) (1)
Sororopan	
Macarena (Columbia)	2615 (8577) (1)
Chiribiquete (Columbia)	910 (2985) (2)

Source #1: Healey, 1993.

Source #2: National Geographic Atlas of the World, Fifth ed., 1981.

Source #3: Int'l. Map of the World, Brazilian Survey ed., sheet NA-19, 1982.

Source #4: Karta Mira, 1966, Sheet 109.

Source #5: 1971 Creole Petroleum Corp. Road Map of Venezuela.

Source #6: Mayr and Phelps, 1963.

Source #7: George, 1991.

Source #8: Huber, 1992.

Source #9: Healey, 1986.

Source #10: Huber, 1993.

wetlands include one or more of the following attributes: 1) the land supports predominantly hydrophilic plants; 2) the substrate is predominantly poorly drained hydric soil; and 3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season (Shaw and Fredine 1956; Cowardin et al. 1979; Zoltai and Pollet 1983; Navid 1989).

Tepui summit vegetation can be divided into the following categories: 1) algae and lichens growing on bare rock; 2) plants growing in shaded cracks and fissures in rock; 3) herbaceous plants and woody subshrubs growing in shallow sandstone depressions (Figure 4); 4) herb-dominated slopes (Figure 4); 5) shrub-dominated slopes (Figure 4); and 6) shrub or small tree forests in gullies and arroyos (Figure 4).

Plant communities 1 and 2 are upland habitats that do not meet any of the wetlands criteria, but the other communities are all wetland types.

Shallow sandstone depressions (#3) are saturated with or covered by water throughout the rainy season, and at times during the dry season (Figure 4). Shallow depressions may have no soil or have various percentages of organic matter mixed with sand that has eroded from the Roraima Formation sandstone substrate. As depressions enlarge during erosion, they become filled with organic matter and are colonized by herbs and woody subshrubs. On gentle slopes where soil has developed, the soil consists of slope-washed sand mixed with an often deep accumulation of partially decomposed organic matter. Soils of gentle slopes, as well as those in shallow depressions, are saturated with water from the abundant rains and mists on tepui summits, and are assumed to be highly acidic (pH 3.5–5.0).

Plant community types 3 and 4, herbs and woody subshrubs growing in shallow sandstone depressions and herb-dominated seepage slopes (Figure 4), also meet the wetlands criterion of supporting predominantly hydrophilic plants. These communities support mixtures of acid-loving wetland genera such as the sundews (*Drosera*), bladderworts (*Utricularia*, *Genlisea*), club mosses (*Lycopodium*), yellow-eyed grasses (*Xyris*, *Orectanthe*), pipeworts (*Eriocaulon*, *Syngonanthus*, *Paepalanthus*), pitcher plants (*Heliamphora*), *Sphagnum*, and others. Associations of these plant genera, which include families of carnivorous plants, define acid seepage bog wetlands the world over (Givnish 1993).

Shrub-dominated slopes (#5) may simply be a late successional stage of herbaceous slopes. These are developed on saturated peat accumulations, up to several decimeters deep (Figure 4). Similarly, shrub and small tree forests in gullies and arroyos (#6) are also developed

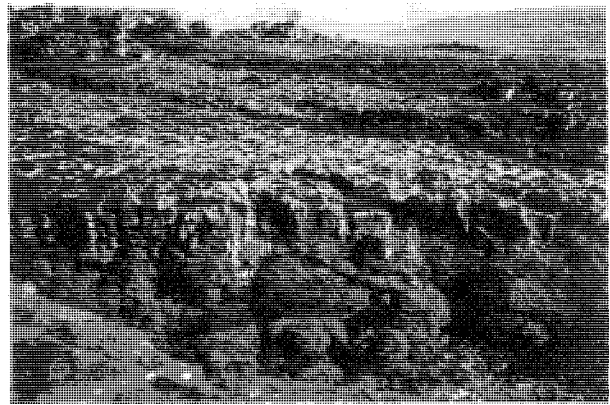


Fig. 4. Interior of Auyantepui looking north from south rim at El Libertador. On the flattish bench in the middle ground are visible Roraima sandstone with water-laden potholes and seepage slope herbaceous wetlands. Shrub-dominated seepage forests clothe the slopes in the distance, and a shrub/tree forest on deep, saturated peat is visible in a protected arroyo in the foreground.

on beds of deep saturated peat (Figure 4). Because of the frequent rains and mists on tepui summits, almost all the soils have a high percentage of organic matter in a saturated state. These are soils of the ombrotrophic bog or fen type (Mitsch and Gosselink 1993), which meet the wetlands criterion of saturated or poorly drained hydric soil.

Tepui flank vegetation can be grouped into 5 categories: 1) cliff-face epiphyte communities; 2) Midland cloud forests, usually on upper talus slopes; 3) streamside and arroyo gallery vegetation; 4) Lowland rainforest on foot-slopes; and 5) successional forest recovering from fire. Successional forest can be in any stage of recovery from bracken-grassland to forests of pioneer tree species. Tepui flank vegetations are mostly upland (=non-wetland) habitats, but the high altitude cloud forests developed on deep, saturated peat qualify as forested wetlands by the criteria mentioned earlier.

FIRES ON TEPUI FLANKS AND SUMMITS

Auyantepui.—The summit of Auyantepui is about 700 km² of flat to ruggedly broken terrain (Brewer-Carias 1987), supporting all the kinds of habitats found on tepuis. During a low flight on 2 March 1992 I saw and photographed from the plane a large burn of at least 50 ha on the summit of Auyantepui about 1.5 km NW of the top of Angel Falls. Blackened dead trunks of shrubs and small trees were obvious from the air. Herbaceous vegetation had replaced what appeared to have been mainly a shrub forest. Judging from the vegetative recovery, the site burned more than one year previously.

This large burn was located far from any human footpath, but helicopter flights are common to this part of the summit from the Canaima tourist camp beyond the NE base of Auyantepui, and climbing and back-packing ascents to the falls have taken place (Nott 1972). It is not known if this fire was ignited by lightning, but the potential exists that it might have been anthropogenic in origin, arising from a campfire or malicious intent.

Looking south from the summit of Auyantepui about 5:00 p.m. on 27 February 1992, I and three companions spotted a fire of about 40 ha burning on the flattish ridge of Midlands elevation called Guayaraca, running south and away from the southwest base of Auyantepui. The fire was burning on both sides of the footpath leading to the summit (pioneered by Felix Cardona Puig in 1937) from the Pemon village of Kamarata. We observed the fire burning for two hours before retiring; by morning, the absence of smoke indicated that the fire had gone out. From 8:00–10:00 a.m. on 29 February, I examined the burn on foot and estimated its final acreage at about 75 ha. In addition to upland savanna vegetation (the grass, *Trachypogon plumosus*, the pipewort, *Paepalanthus capillaceus*, and sedges), a 2-ha wet prairie (hillside seepage bog) burned completely. The wet prairie contained *Drosera roraimae*, *Brocchinia reducta*, and a *Utricularia* species, all carnivorous wetland plants.

Several hectares of rainforest were killed at the margins of the savanna where the fire was able to run into the forest over flat or unobstructed terrain. An island (ca. 1 ha) of rainforest in the burned savanna had been protected by steep slopes and rocky terrain leading into the forested habitat patch. Rocky outcrops, wet soils or a break in the terrain marking steep slopes, seemed to lie along most of the rainforest/savanna interface, protecting the rainforest from the incursions of fire.

In Kamarata on 2 March 1992 I was told by Professor Gerd-Alois Zwing of Nürnberg, Germany, that the fire on the trail to the summit of Auyantepui had been set by two guides he had employed from the village. Zwing said he was surprised when the Pemon men “purposefully set the fires rather maliciously,” lighting the dry grasses by match in two places after they descended from Auyantepui. He could determine no reason for their actions.

On Cardona’s foot-trail ascending the talus slope at the base of the fringing cliffs of Auyantepui, I have witnessed and photographed a few dead standing and many downfallen stems of hardwood trees, indicating the one-time presence of a rainforest such as the one clothing the steep slope between the lower edge of the talus slope and the ridge below it where I witnessed the fire on 27 February 1992.

This is the same talus slope about which Tate (1938) said, “Until ten or fifteen years ago a large part of the south slope was clothed with tall forest. However, in some unusually dry year—not improbably when the forests of Roraima and the Kaieteur area were destroyed—savanna fires, which in the dry season are wantonly kindled by natives, driven up the slopes by the strong southeast trades blazed up the tindery lines of fern and moss growing in every crack in the precipices and annihilated about four-fifths of the plateau vegetation. Hence most of the south slope from 1500 to 2000 meters today carries either shrubby or herbaceous second-growth flora entirely distinct from the rich, moist forests of former times.”

One would not expect that the dead tree trunks I observed in 1988 date to the fires cited by Tate. Termites, fungi, bacteria, arthropods, and subsequent fires all would seem to work rapidly to disintegrate dead trees in a tropical climate. It is possible that this slope has burned periodically in the past 50 years so that trees surviving early fires were killed eventually by later fires, resulting in the dead standing trees I saw. Otto Huber (in litt.), however, stated that unpublished information gathered by Electrificación del Caroni, C. A., indicates that trunks have been standing dead on this slope for more than 40 years.

On 23 February 1992 I photographed a burned area of about 4 ha in shrubby vegetation, about 2 hrs hiking N into the summit terrain from El Libertador. El Libertador is a place at the edge of the south cliff of Auyantepui where a bust of Simón Bolívar marks the top of the trail to the summit pioneered by Felix Cardona Puig. This patch was not burned when I first passed through it on 29 December 1988. At that time the “trail” was marked by small rock cairns on bare terrain and some old orange surveyor’s flagging tied to bushes. I lost my way often. In 1992 the trail was wide and deeply rutted into the organic soil, indicating its interim use by a large number of backpackers. Dated graffiti on the rocks of rock shelters corroborated this. Considering the heavy foot traffic and that people from local villages have a proclivity for careless woods burning as demonstrated by the above example, it is highly likely that this fire was anthropogenic in origin.

The flanks of Auyantepui are vegetated in dense rainforest everywhere but the south end of the massif, which overlooks the village of Kamarata, occupied by Capuchin monks ca. 1940. Fires set by villagers frequently burn up the flanks of Auyantepui here (Figure 5), and it is reasonable to hypothesize that all of the open grassland on the south flanks of Auyantepui and possibly much of La Gran Sabana at its base are of anthropogenic origin.

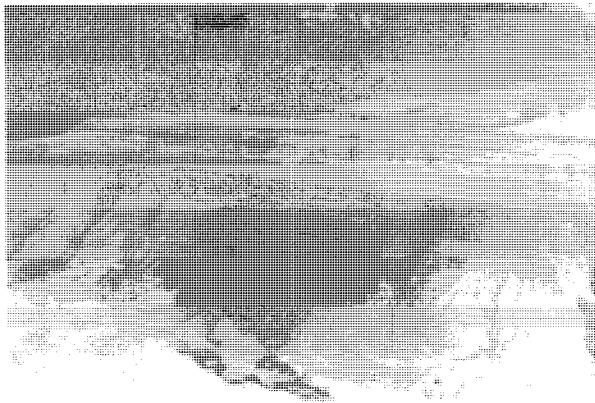


Fig. 5. Fire mosaic of forest and savanna on flanks of Auyantepui, 1992.

Duida.—On 29 January 1991 I hired two men from the Yekwana village of Culebra to guide me and three others to the summit of Pico de Culebra, a high point at the north end of Cerro Duida overlooking the village, one of the largest tepuis of the Guayana Highlands, with a summit area of about 1,100 km². On the ascent the men led us up a hogback ridge through rainforest with no trail. Apparently they had forgotten how to find the existing trail located on another ridge about 1 km to the east, which we later descended, or they had some reason to ascend by a new route. At about noon on 1 February 1991, while camped near the edge of the escarpment overlooking the ridge we ascended, I noticed that the rainforest at the top of the ridge was burning, and fire was backing down from the summit over a steep rocky slope heavily vegetated with bromeliads and other epiphytes. Altogether about 2 ha were burned (Figure 6). Our guides heard us complaining that fires in this vegetation are bad, so the next day, while observing the burned area from the old trail on the eastern ridge while we descended, the head guide volunteered that the fire was caused by lightning. This was unlikely because for the past three days and nights there had not been a cloud in the sky. Later, we learned from two teenage sons of our guides who had accompanied us on the ascent, that they, themselves, had deliberately ignited the fires to “clean up” the trail.

Both the summit of Pico de Culebra and the top of the ridge with the original trail are devoid of trees and vegetated with herbaceous vegetation. All the rest of the nearby tepui flanks, ridges, and summit are clothed in dense forests. Charcoal and fire scars on woody shrubs and trees at the edges of these clearings make it likely that the treeless areas were once forested and have been converted to grassland by anthropogenic fires in the past century. A small savanna of about 20 ha surrounding an airstrip between the village of Culebra and the foothills of Cerro Duida is no doubt of anthropogenic origin, associated with human activity in the village.

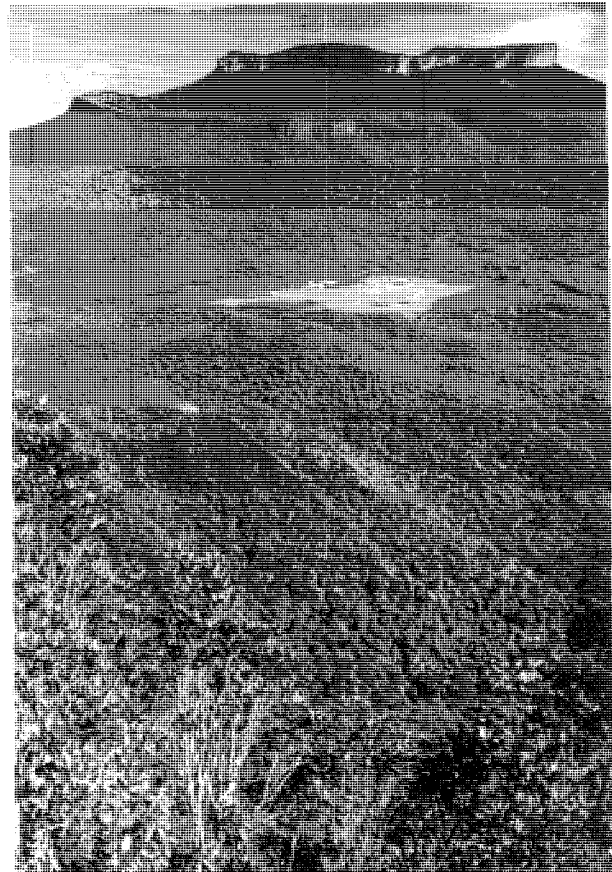


Fig. 6. Two-ha burned crest of a ridge leading north off of Pico de Culebra, north flank of Cerro Duida; a plume of smoke is visible, 1991. A small anthropogenic savanna is maintained as an airstrip adjacent to the Yekwana village of Culebra (black patches are recently burned patches in it). Rainforest in varying stages of recovery from slash and burn agriculture is visible as multi-textured patches along the Rio Cunucunuma. Cerro Huachamakare, a small tepui, rises in the background.

In the afternoon of 2 February 1991, as we were returning to the village of Culebra from Pico de Culebra, we passed a village woman and a 5- or 6-year old boy who had ignited about a half dozen small fires in the second-growth forest beyond the south edge of the Culebra savanna. The little boy followed us across the savanna with a flaming torch in his hand, igniting four patches of fire in the grass before we reached the airstrip. At dusk of the same day, I watched children gather in small groups and set fires in the open grassy areas all around the village for about two hours.

The next day I interviewed Francisco Diaz, one of the chiefs of the village who had been one of our guides, about fire. He said that the children set fire to the woods for play. People set fire to the forest along trails that they walk “por limpio” (to clean them). He admitted that his sons had ignited the fire on the new route we used on our ascent of Pico de Culebra. He said he saw no harm in burning.

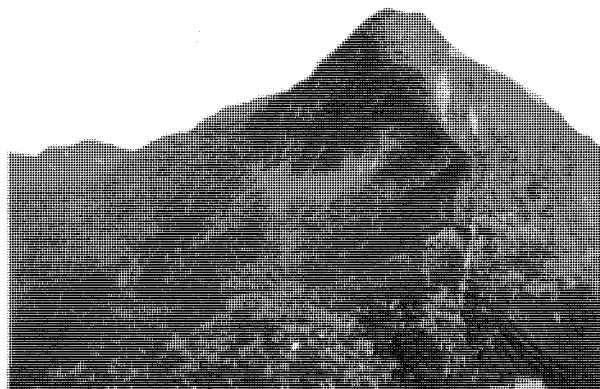


Fig. 7. Aftermath of fire on south rampart of Cerro Duida, 1992.

On 22 November 1991 I camped in a large burned area near the summit of the southernmost ridge leading south down from the southern flank of the Duida massif overlooking the Catholic mission at La Esmeralda. The burned site of about 100 ha lie astride a difficult passage up the south flank of Cerro Duida that was established in 1979 by an expedition from the Venezuelan Universidad de Oriente (Figure 7). My guide, Rafael Maita, a resident of La Esmeralda, told me that the fire had been set two weeks earlier by villagers who had been portering for a botanical expedition from Kew Gardens, London. Their purpose was to remove vegetation to make walking easier.

The vegetation of this exposed hogback ridge was a dense groundcover of bromeliads (*Brocchinia* spp.), bracken fern (*Pteridium aquilinum*), grasses, and scattered shrubs, including tyty (*Cyrilla racemiflora*). Near the top of the ridge close to the summit of Duida were patches up to 10 m² of the sun pitcher (*Heliophora tatei*). On the way down from the summit 18 days later on 10 December, I observed that most of these plants were alive and were putting up new leaves (*Heliophora*, *Pteridium*, *Brocchinia*) or resprouting from their bases (*Cyrilla racemiflora*).

The fire, while devastating on the steep ridge, did not penetrate more than a few tens of meters onto the flatter terrain of the summit. The summit vegetation is a dense mixture of herbaceous plants and woody subshrubs, up to one meter high, growing on deep (0.5–2.0 m), saturated peat. In one 10 m × 40 m transect within 200 m of the burn, I counted 83 species (Table 2). Taller woody vegetation on the high rim of Cerro Duida is confined to protected valleys.

From 27 November–4 December 1992, Will Ryan and I walked north into the interior of Cerro Duida from its southern rim. In eight days we covered only about 15 km, walking in wetlands vegetation the entire way.

Table 2. List of plants scored on a 10 m × 40 m plot on the south summit of Cerro Duida, elevation ca. 2300 m, 26 November 1991.

Family or group	Genus or growth habit	Total species
Lichens	<i>Cladonia</i> , <i>Usnea</i> , etc.	8
Musci	mosses	1
Sphagnidae	sphagnum moss	2
Lycopodophyta	<i>Selaginella</i> , <i>Lycopodium</i>	3
Pterophyta	ferns	6
Eriocaulaceae	herb	1
Xyridaceae	<i>Xyris</i> , <i>Orectanthe</i>	2
Rapateaceae	<i>Stegolepis</i> spp.	2
Cyperaceae	sedge	1
Poaceae	grass	1
Bromeliaceae	3 epiphytic; 4 terrestrial	7
Orchidaceae	orchids	8
Lentibulariaceae	<i>Utricularia</i> , <i>Genlisea</i>	3
Araliaceae	<i>Schefflera</i> sp.	1
Droseraceae	<i>Drosera</i> cf. <i>roraimae</i>	1
Sarraceniaceae	<i>Heliophora tatei</i>	1
Loranthaceae	mistletoe	1
Ericaceae	shrubs	4
Theaceae	shrubs	2
Cyrtillaceae	<i>Cyrilla racemiflora</i>	1
Melastomataceae	3 shrub spp.	3
Rubiaceae	shrub	1
Leguminosae	herb	1
Lauraceae	shrub	2
Burmanniaceae	herb	1
Compositae	shrubs	3
Unid. vine		1
Unid. shrubs		≈15
Total species		83

Ridge crests were vegetated with herbaceous bogs or shrub bogs developed on saturated peat. They contained all the plants listed in Table 2, plus many others, including several species of terrestrial bromeliads (*Brocchinia* spp., *Navia* sp., *Brewcaria duidensis*), orchids, species of Rapateaceae, and a species of sun pitcher, *Heliophora* sp., up to eight feet tall. Interior slopes were very steep and contained patches of open herb bogs intermixed with stands of dense shrubs or small trees of the genera *Bonnetia*, *Cyrilla*, *Ilex*, *Clusia*, *Schefflera*, *Weinmannia*, *Tyleria*, *Mikania*, and others. The soil under shrub and small tree forests was deep, saturated peat, up to 1.0 m deep.

We made our way into the densely vegetated tepui by working down into a deep gorge which flowed north into the interior. At the bottom of the gorge and about 2.0 km from the south edge of Cerro Duida, we encountered a gallery rainforest of apparent similar composition as the "talus slope" and "steep slope forests" on the flanks of Cerro Duida described by Gleason (1931). During our entire voyage on foot, we did not notice any evidence of fire, but I concede that 1) we were confined mostly to walking down the stream bed of a deep interior valley where fires are not likely to reach, and 2) heavy rainfall and regrowth might obscure the evidence in about one year's time. It is also worth noting that except for the torrent-swept stream beds, even on ridge crests, rocks

and bare mineral soil were rarely seen because they were buried in deep, saturated peat.

Fires of anthropogenic origin may have burned the southern face of Cerro Duida since the occupation of Esmeralda by Spanish missionaries in 1768 (Iribertegui 1987). Humboldt's observation in 1800 about the existence of the savanna at Esmeralda was verified by Schomburgk (1840), who stated, "Thirty-nine years had elapsed since Alexander Von Humboldt visited Esmeralda . . . Nature, however had remained the same; Duida still raises its lofty summit to the clouds, and flat savannas, interspersed with tufts of trees and the majestic *Mauritia* palm stretch from the banks of the Orinoco to the foot of the mountains. . . ."

Tate and Hitchcock (1930) said of the Cerro Duida region, "Most of the land is forested," but "Fire has passed through considerable portions of the forests here, leaving nearly impenetrable tangles of fallen logs overgrown by *Heliconias* and vines . . . A low ridge called Guaraco, with scarp facing the Orinoco, parallels the southwestern cliffs of Duida. From fissures in this hill fire is reputed to appear every year during January and February. Two other places on the cliffs of Duida itself were pointed out as the spots where, even after heavy rain, fire always starts. This idea of mysterious light has been carried down from the days when Humboldt first visited Esmeralda . . . During five and a half months' stay in the Duida region there was no mysterious beacon, and the only clues to the story are portions of slope burnt over by forest fires."

Reporting on the Tyler-Duida Expedition, Gleason (1931) said, "The largest burned area extended from around Middle Camp up a great part of the talus slope and precipitous part of one of the southern promontories called by us Burned Mountain and, as found subsequently, actually reached the summit of the plateau."

From the south summit of Duida on 23 November 1991, I photographed the full extent of La Esmeralda savanna (Figure 8). It was streaked with recent fires, parts still smoking. While fires are most likely to be kindled in the dry season, indigenous peoples burn all year round, whenever the fuel permits ignition. The savannas are burned in a mosaic fashion so that fires are likely to sweep into the fringing rainforests at any time of year, and sometimes more than once a year.

Neblina.—Remote Cerro de la Neblina, first reached by an expedition in 1954 (Maguire 1955), was the focus of a four-year long series of international expeditions, 1983–1987 (Brewer-Carias 1988). Expedition members discovered two plateaus on the north side of Cerro de la Neblina, approximately 2 km² in area (1,750 m elevation), that had burned sometime about November

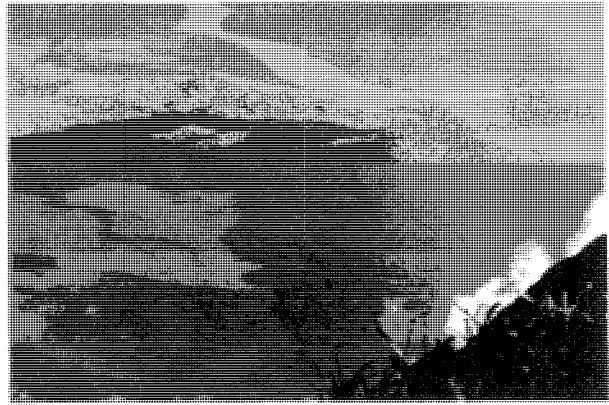


Fig. 8. La Esmeralda savanna looking SE from the summit of Cerro Duida, 1992.

1984 (Givnish et al. 1986). The fires appeared to have been ignited by lightning because frequent lightning strikes were observed in the area, no humans resided within at least 10 km of the tepui, and the sites were isolated from the lowlands by cliffs (Givnish et al. 1986).

Roraima, Kukenan, and La Gran Sabana.—The tops of the high elevation tepuis with small summit area (< 10 km²) are rocky and patchily barren, so that naturally ignited summit fires must be rare and of limited acreage, in spite of the high incidence of lightning strikes. Small patches of summit vegetation near the cliff edges of these tepuis might burn during the dry season when fires started in the foothills and in the plains of the surrounding Gran Sabana burn through talus slope forests and up the sometimes thick epiphytic vegetation growing on the cliff faces. On two summit explorations of Roraima (1987, 1990) and one summit exploration of Kukenan (1992), I saw no signs of recent fires in interior summit vegetation, but evidence of devastating fires was abundant on talus slopes and foothills (Figure 9) which have had a long history of burning. Vast rainforest acreage in the vicinity of these two famous tepuis has been deforested by anthropogenic fires in this century.

Tate (1930) was the first naturalist to lament the deforestation of the flanks of Mt. Roraima: "The lowlands about Roraima are scantily peopled by the Arekuna (Jarecuna of Brazil) Indians who inhabit the basins of the Cotinga, Kukenam, and Caroni rivers. They have a deplorable custom of setting fire to the grasslands of their territory. The fires sweep over hundreds of acres of savanna annually, and, entering the forests, destroy or greatly alter the component vegetation of large tracts. Great regret was felt on finding that two years before the arrival of the expedition, during a period of extreme drought, the greater part of the forests of the diabase slopes of Roraima had been completely destroyed. The fire had even reached the plateau by way of the ledge but had made no progress in the scanty vegetation. On

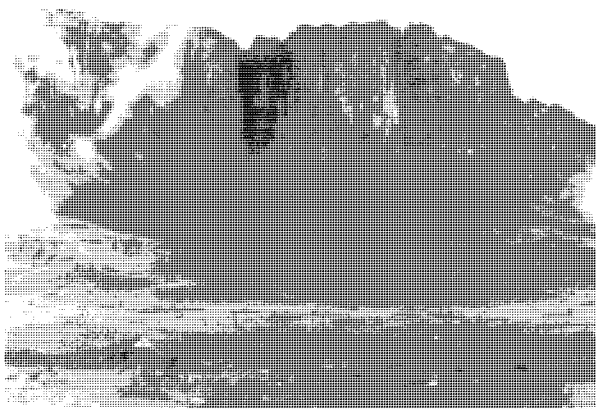


Fig. 9. Deforested foothills and talus slopes of Cerro Kukenan, 1992.

the slopes surviving pockets of forest at various altitudes were discovered for the assemblage of collections representative of the rich fauna and flora that existed before the fire.”

Beard’s (1953) observations are equally graphic. “Nearing the base of Roraima, many of the patches of forest are seen to have been overrun by fire and are now fringed by dead trees or even consist entirely of groves of blackened trunks. . . .” In the vicinity of Roraima, Beard says, “The aboriginal population is thus extremely small, perhaps averaging one person per 10 sq. mi. None the less they manage very thoroughly to set fire to the savannas every year. Grass seems to be regularly fired as soon as it gets long enough and full of enough dead trash to burn. These savannas are swept by strong breezes and dead grass dries rapidly after rain so that a fire can be set at almost any time though of course the dry season provides best conditions. The writers’ three Indian carriers, on being allowed to have matches, set fire to the grass along the trail several times a day, whenever a patch of tall grass was crossed. When questioned they were unable to give any coherent reason for their actions. It is probable that basically the desire is to keep the country open. Other wandering Indians were evidently doing likewise for columns of smoke were often seen and later, from the camp site on Roraima overlooking the Gran Sabana, many grass fires could be seen blazing at night.”

On each of my three trips to Roraima and Kukenan (1987–88, 1991, 1992), I saw many fires burning in the savannas leading to the mountains; I observed Pemon Indians actually igniting fires; and I observed hundreds of hectares of deadfallen and standing trunks on the foothills leading to the bases of each mountain (Figure 9). On 15 January 1991 I photographed Uei Tepui (Figure 10) from a position about 25 km to the northwest, on the footpath to Roraima from the Pemon village of Peraitepui. The vegetation between my position and Uei

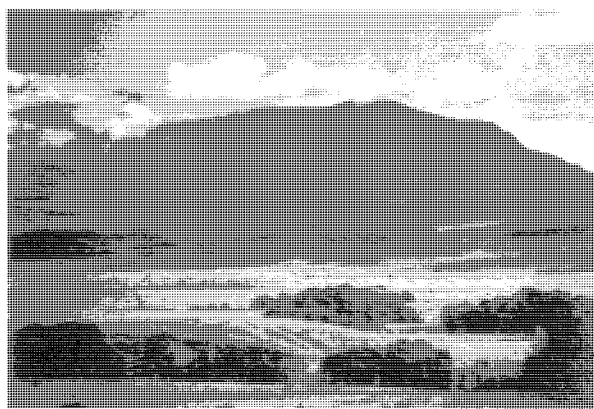


Fig. 10. View across La Gran Sabana to the summit of Uei Tepui, originally rainforest, now savanna, 1991.

Tepui was savanna grassland all the way to the summit of Uei Tepui. This was not the case about sixty years earlier, however, as a reading of Tate (1930) reveals.

“On the eastern side of Roraima a station was formed at Arabupu, 4000 feet, where forests have been less injured and environmental conditions are essentially the same as must have prevailed at Paulo before the fire . . . A mile or so to the north of the village, however, the grasslands terminate. To the southeast after half an hour’s walk from camp the border of the great forest of Weitipu, stretching unbroken for some ten miles to the northern slopes of the mountain of the same name, is reached.”—Tate (1930).

Thirty-seven years later Mayr and Phelps (1967) had this to say about Uei Tepui: “Only patches of forest remain, because most of the slopes have been burned.”

Fire records for other tepuis.—No published data about fires exist for many large tepuis or tepui massifs (Guanacoco, Guaiquinima, Chimantá, Jaua-Sarisariñama, Aracamuni, Avispa, Parú, Cuao-Sipapo). Frequent fires might be expected in the vicinity of a number of small tepuis in northern Estado Amazonas (Camani, Yavi, Guanay, Yutajé). These tepuis occupy a small region of lower rainfall and longer dry season (MARNR 1985). Several small savannas are located immediately south of these tepuis in the upper reaches of the Rio Manapiare drainage basin (Huber and Alarcon 1988), and the region is fairly heavily populated by Piaroa and other indigenous peoples.

During a survey of the bird life of tepuis, Mayr and Phelps (1967) commented on fires throughout the Guayana region, and published some photos of the aftermath. “During the last 50 years there have been several pronounced dry seasons when fires destroyed part of the vegetation of the tepuis (plate 15, figure 2; plate 16, figure

1; plate 17, figure 2). In the 1920's the slopes of Roraima, Sororopan-tepui, Auyan-tepui, and others were seriously burned as far up as the cliffs, and in 1947 the vegetation of the lower slopes of Cerro Yavi was also consumed by fire, endangering the members of the Phelps Collection expedition whose camp was in the path of the flames. Seldom do these fires start from natural causes; they are started by the Indians who, now that they can make fire easily with matches, frequently set fire to savannas to signal their presence to other Indians or sometimes merely for amusement."

Sororopan-tepui: "Fire destroyed much of the vegetation of the southern slopes about 40 years ago." Upuigma-tepui: "Periodic burning by the Indians has left only sparse vegetation on most of the slopes, which has in turn undoubtedly reduced the number of species of birds to be found there to the present time."—Mayr and Phelps 1967.

Mayr and Phelps (1967) also recorded valuable observations about unburned tepuis whose slopes were still heavily forested: "Ptari-tepui was saved from this disaster because the fire came from the savannas on the east and south, consuming the forest cover to the summit of Sororopan-tepui, where it died out, thus leaving intact the entire talus vegetation of Ptari-tepui." Uaipan-tepui: "Most of the talus is forested and has not been burned." Chimantá-tepui and Acopan-tepui: "This extensive tepui, with intact, unburned talus slopes, varied vegetation, and upland streams. . . ."

Esias Rodriguez, one of the chiefs of the Yekwana village of Cacuri, gave me a surprisingly sophisticated answer about why Yekwana people burn the Guayana Lowlands savannas on the middle Rio Ventuari. Rattlesnakes had killed his eight-year old son and bitten his wife in the past. He said, "There are few snakes in the forest, but many 'cascabeles' [=neotropical rattlesnake, *Crotalus durissus*] are encountered in unburned savanna when it grows thick with grasses. When the savanna grass goes long unburned, the 'conejos' [=rabbits and/or small rodents] become abundant, which thereafter makes rattlesnakes abundant."

This is a very reasonable motivation for burning savannas, if it is true, but the expansion of savannas at the expense of rainforest only creates more habitat for rattlesnakes, which are not rainforest creatures. Rainforests are not snake-infested environments, and South American venomous snakes, while numerous in species, generally are rare in local abundance (Means 1994). Ironically, the expansion of savanna at the expense of rainforest due to increased burning in post-Columbian times may actually achieve the very end result that Rodriguez claims is the reason for burning.

CONCLUSIONS

From the limited information provided in this paper, it is obvious that fire is important in the ecology of the Guayana region. No systematic survey of fire incidence has been conducted on the summit of any tepui, but there is evidence for summit fires on at least some of the larger tepuis. Whether these were ignited naturally by lightning is unclear. Lightning-ignited fires on tepui summits appear to be rare. Increasing visits to tepui summits by backpacking expeditions, however, almost always involving Amerindian guides hired from local villages, threatens an increase of anthropogenic fires on tepui summits.

The literature and my own observations indicate, however, that anthropogenic fires are common in the savannas at the bases of tepuis and on tepui flanks, especially where tepuis rise from La Gran Sabana in Estado Bolivar. Fires in the savannas of the Guayana region are presently being ignited at such a high frequency that fuel rarely accumulates in large patches before a match is tossed into it. On my first and second hikes over the 25-km trail to the base of Mt. Roraima in 1987–88 and 1991, patches of unburned savanna vegetation dominated the entire panorama, up to 1.5 m tall. Several times when I made forays off the footpath, I had to struggle to pass through the dense bracken, grasses, and sedges. On 9 December 1992, however, I was amazed that the savanna as far as I could see over the entire length of the footpath was burned to the bare ground. Green new growth was nowhere more than 5.0 cm high, indicating that thousands of hectares had been burned before the normal dry season had commenced (in late December and January). I made forays up to 1.0 km from the footpath and encountered no unburned grassland patches.

Writing about these same grasslands more than half a century ago, Myers (1936) said, "By far the greater portion of these savannas, both on the Rio Branco-Rupununi plains and in the mountains, is still in a primitive condition. The main influence of man has taken the form of fire, but it is by no means certain how frequent grass fires were before human intervention. . . . The scattered aboriginal Indians are inveterate burners. It is almost impossible to prevent one's Indian carriers from setting light to the dry grass. They do this to signal their approach and for pure fun. I have never seen in South America a savanna however small or isolated or distant from settlement which did not show signs of more or less frequent burning."

Frequent savanna fires are a threat to the rain- and cloud-forests on the flanks of tepuis. Everywhere in the Guayana region where there are no savannas near the bases of tepuis, tepuis are densely vegetated by forests.

Where savannas occur near tepuis, the savanna vegetation often runs up the tepui flanks to the cliffs fringing the summits. In my opinion, most, if not all, of the treeless tepui flanks have been created by anthropogenic fires in the past two centuries, since the first contact between European man and South American indigenous peoples.

Evidence for anthropogenic fires is overwhelming, but there remains the interesting question of whether natural fires ignited by lightning have been responsible for some percentage of the present extent of La Gran Sabana, or to have been a selective agent, over the millennia, molding specific fire adaptations in the tepui biota.

Givnish et al. (1986) believe that *Neblinaria celiae*, a rosette shrub (Theaceae) endemic to the summit of Cerro Neblina, has a set of adaptations to fire, which includes the following: a) it is highly fire-tolerant with a measured post-fire survival rate of 93% vs. 0% in seven co-occurring woody species growing on the same site; and b) its growth form involves sparse branching, massive terminal leaf rosettes, and thick bark (Figure 11a).

Other plants in the Guayana Highlands have what appear to be similar morphological adaptations to resisting mortality by fire. Besides *Neblinaria celiae*, several plants in diverse families, monocots and dicots, have insulative leaf parts surrounding their exposed aerial stems. The tepui sundew, *Drosera roraimae* (Droseraceae), retains the petioles of its dead leaves which make a thick insulation around an upward growing stem (Figure 11b). This is a marked departure from the normal habit of a procumbent rosette in the Droseraceae. Many species of *Stegolepis* and *Saxofridericia* (Rapateaceae) retain the dead sheaths of their straplike leaves clasped to the stem. I have seen *Stegolepis guianensis* recovering from fires in which the loose parts of the dead leaves were incinerated, but the sheaths were only slightly charred (Figure 11c). *Vellozia tubiflora* (Velloziaceae) has a densely hairy stem that protects the plant from heat (Figure 11d). I photographed a stand of it which appeared to have survived the fire I witnessed 27 February 1992 on the bench below the summit of Auyantepui.

The unusual bromeliad, *Ayensua uaipanensis*, has a growth form almost identical to *Neblinaria celiae*, of thick, scaly stems covered by old leaf bases (Figure 12a). The stems grow upward from the ground and are unbranched with stiff leaves whorled apically around the end of the stem. Givnish et al. (1986) pointed out that most of the dozen or so species of *Chimantea* (Compositae) (Figure 12b), and at least two other theaceous shrubs (*Neogleasonia*, *Neotatea*) also have growth forms functionally similar to those of *Neblinaria celiae*, all of which they suggested might be anti-fire adaptations.

Another mechanism which protects stems and buds of tepui plants is water in leaf axils or in tubular leaves. Bromeliads abound on tepuis and many have so much water stored in leaf axils that fires cannot reach the stem nor burn off all the leaf tissue. I personally witnessed the recovery of more than 100 *Brocchinia tatei*, a large tank-type bromeliad, the distal portion of whose leaves had been burned off during the flank fire I observed on Cerro Duida. I descended the burned ridge 18 days after my ascent and did not see a single tank bromeliad that had not survived the fire, which was hot enough to kill two- and three-inch diameter stems of shrubs such as *Cyrilla racemiflora*.

Tank bromeliads are common in non-pyrogenic forests throughout the New World tropics, and I do not advance their habit of containing axillary water as an anti-fire adaptation. It is interesting, however, that *Orctanthe sceptrum* of the family Xyridaceae (Figure 12c) is another common tepui plant with a basal rosette of leaves holding water in the axils. To my knowledge, this is the only member of the Xyridaceae whose leaves are whorled around the stem and hold water as in tank bromeliads. Xyridaceae, generally, survive fires in bog habitats from the southeastern U.S. to Venezuela because their stems are protected by tightly clasping spongy or fleshy leaf bases.

On the edge of the summit of Cerro Duida I saw fire-scorched tubular leaves of the carnivorous sun pitcher, *Heliophora tatei*, yet the leaf bases were alive below the water line. Apparently the rhizome is protected by the water-filled leaf bases which clasp the rhizome. Seventeen days later I photographed new leaves growing from the rhizomes through the mass of scorched leaves. Roy McDiarmid photographed this same phenomenon on Cerro Neblina (Figure 12d).

Some species of bromeliads of the genus *Brocchinia* (*B. reducta*, *B. hechtioides*) have evolved true carnivory (Givnish et al. 1984). This is achieved by holding the leaves nearly vertically, so that the erect leaf rosette forms a cylinder partially filled with water (Figure 13). These conspicuous yellow-leaved plants are commonly distributed in wet savannas or bogs on wet sand throughout the Guayana Highlands above about 1200 m elevation. I have observed the survival of most of the *Brocchinia reducta* plants growing on several large wet prairie bogs in La Gran Sabana and in the 2-ha bog I observed after a fire below Auyantepui. Apparently the water in the cylinder assists the carnivorous *Brocchinia* in surviving fires.

One very common bromeliad I observed on Cerro Duida and Auyantepui, *Brocchinia acuminata*, has taken to extremes the putative protection of its stem by water held in its leaf axils (Figure 14). It is a bulbous plant



Fig. 11a. *Neblinaria celiae*, from summit of Cerro de la Neblina.

Fig. 11b. *Drosera rorimae*, from Guayuraca Ridge leading away from southwest flank of Auyantepui.

Fig. 11c. *Stegolepis guianensis*, from summit of Mt. Roraima.

Fig. 11d. *Vellozia tubiflora*, from summit of Pico de Culebra, north rampart of Cerro Duida.



Fig. 12a. The bromeliad, *Ayensua uaipanensis*, showing possible anti-fire growth form, Auyantepui.
 Fig. 12b. *Chimantaea* sp. showing possible anti-fire growth form, Chimantá.

Fig. 12c. *Orectanthe sceptrum*, Roraima.
 Fig. 12d. *Heliampora* sp. recovering from fire, 1984, summit of Cerro Neblina.

whose long leaves are quite wide for the first one-third of their length, then taper into a narrow acuminate distal two-thirds. The straplike distal parts of the leaves are whorled away from the stem as is normal in most bromeliads, but the broad lower parts of the leaves tightly

clasp the stem, overlap each other, and hold a large quantity of water in each axil. A one-meter high specimen yielded about two liters of water. All of about 20 of these plants had survived on the burn I examined on the south flank of Cerro Duida.

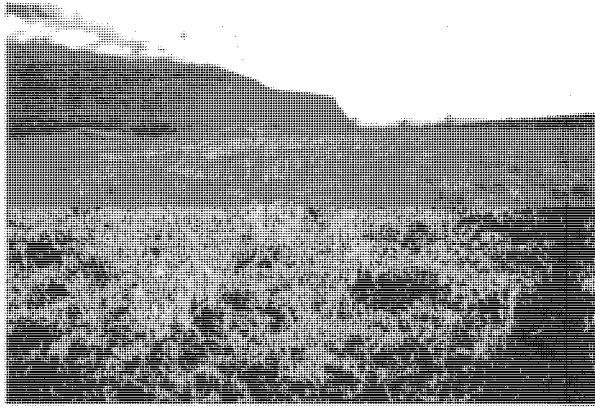


Fig. 13. *Brocchinia reducta* growing on a wet savanna on Guayuraca Ridge at the southwest base of Auyan-tepui, 1992.

It is difficult to deny that what appears among many different plant families to be convergent evolution on thick, corky, densely hairy, or water-protected stems are adaptations to resist death by fire. Only in parts of fire-prone Australia are there so many different plants with putative anti-fire adaptations. It can be argued, however, that most of these adaptations are mechanisms for the conservation of water. Dry seasons and occasional droughts, even in the present climate of the Guayana region, may be periodically so severe that water conservation is necessary on tepui summits and in the Lowlands and Midlands where many of the acid bog loving plants also grow. Many tepui summit plants show water conservation morphologies that are not anti-fire adaptations, such as thick, tiny, coriaceous leaves (*Tepuia* spp., *Notopora* spp., *Ledothamnus* spp., *Bonnetia roraimae*, *Habenaria roraimae*, *Mallophyton chimantensis*, *Maguireothamnus speciosus*, and many others) or densely hairy leaves (*Macairea cardonae*, *Raveniopsis tomentosa*). When the sun comes out and the wind blows, water stress can be high on tepui tops. During the Pleistocene, the climate of South America is thought to have been dryer (Rull 1991), so that selection for water conservation morphologies in plant parts would have been much stronger.

Water conservation goes hand-in-hand with anti-fire strategies, however. Drought, dry climate, and heat are conducive to increased fire frequency. Moreover, plants on tepui summits are not necessarily restricted to summit elevations. Many of the plants discussed above are wide-ranging in the Midlands of La Gran Sabana, occurring there in wet prairie bogs as well as on tepui summits (e.g. *Brocchinia* spp., *Stegolepis* sp., *Heliamphora* spp., *Drosera roraimae*, *Orectanthe sceptrum*, *Utricularia* spp.). Although not found on tepui summits, it is worth noting that two dominant grasslike plants of frequently burned La Gran Sabana upland habitats, *Paepalanthus capillaceus* (Eriocaulaceae) and a sedge, *Bul-*



Fig. 14. Bottle shaped bromeliad, *Brocchinia acuminata*, summit of Cerro Duida, 1991.

bostylus paradoxa, have dense, woolly procumbent stems that are always blackened with charcoal; these plants sprout new leaves vigorously almost immediately after fire (Myers 1936, pers. obs.).

Finally, during drier times in the Pleistocene, tepui biota may have migrated downward in elevation (Rull 1991) onto the Gran Sabana plains and other middle elevation landforms. It is not necessarily in today's climate that we should look for the selective forces that have shaped the adaptations of the world's biota.

Reasons for the rapidly diminishing rainforests of the world usually are economic (extraction of resources, agriculture, living space), but in the Guayana region where human population density has remained low and access by outsiders has been limited, some rainforest destruction has proceeded at a slow pace over the past two centuries for little better reasons than "cleaning trails," "removing snakes," or for fun. Now, however, both estados Bolivar and Amazonas are opening up to internal colonization from other Venezuelan states, and the indigenous population is burgeoning (Anonymous 1993). The time is ripe for ecologically correct environmental education aimed at changing the attitudes and practices

about indiscriminant burning of savanna and woodland by the peoples living in the Guayana Highlands.

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LITERATURE CITED

- Anonymous. 1993. Censados en Venezuela, 314.772 indigenas. Tiempo de resultados 2. Oficina Central de Estadística e Informática. Caracas.
- Beard, J. S. 1953. The savanna vegetation of northern tropical America. *Ecological Monographs* 23(2):149–215.
- Bisschops, J. H. 1969. The Roraima Formation in Surinam. *Verh. K. Ned. Geol. Mijnbouwkd. Genoot. Geol. Ser.* 27:109–117.
- Brewer-Carias, C. 1987. The lost world of Venezuela and its vegetation. Caracas.
- Brewer-Carias, C. 1988. Cerro de la Neblina; Resultados de la expedición 1983–1987. Caracas.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U. S. Fish and Wildlife Service Publication FWS/OBS-79/31. Washington, D. C.
- Fischer, W. C. 1980. Index to the Proceedings of the Tall Timbers Fire Ecology Conferences: Numbers 1–15, 1962–1976. USDA Forest Service Technical Report INT-87:1–140.
- Gansser, A. 1954. The Guiana Shield (S. America), Geological observations. *Eclogae Geologicae Helveticae* 47:77–112.
- Gansser, A. 1974. The Roraima problem. *Verhandl. Naturf. Ges. Basel.* 84:80–100.
- George, U. 1991. *Inseln in der Zeit.* Geo im Verlag, Hamburg.
- Ghosh, S. 1977. Geología del Grupo Roraima in Territorio Federal Amazonas, Venezuela. *Mem. 50 Congreso Geol. Ven.*, 167–173.
- Gibbs, A. K. and C. K. Barron. 1983. The Guiana Shield reviewed. *Episodes* 1983(2):7–14.
- Givnish, T. J. 1993. Ecology and evolution of carnivorous plants. Pages 243–290 in W. Abrahamson (ed.). *Plant-animal interactions.* McGraw-Hill Co., New York.
- Givnish, T. J., R. W. McDiarmid, and W. R. Buck. 1986. Fire adaptation in *Neblinaria celiæ* (Theaceae), a high-elevation rosette shrub endemic to a wet equatorial tepui. *Oecologia* 70:481–485.
- Givnish, T. J., E. L. Burkhardt, R. E. Happel, and J. Weintraub. 1984. Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient-poor habitats. *American Naturalist* 124(4):479–497.
- Gleason, H. A. 1931. Botanical results of the Tyler-Duida Expedition. *Bulletin of the Torrey Botanical Club* 58:277–506; 555–562; 1 map, plates 17–44.
- Gleason, H. A. and E. P. Killip. 1939. The flora of Mount Auyan-tepui, Venezuela. *Brittonia* 3:141–204.
- Healey, K. 1986. South America Northwest, International Travel Map, First edition, 1986–87.
- Healey, K. 1993. South America Northwest, International Travel Map, Second edition, 1993–95.
- Huber, O. 1990. Estado actual de los conocimientos sobre la flora y vegetación de la region Guayana, Venezuela. Pages 337–386 in F. H. Weibezahn, H. Alvarez, and W. M. Lewis, Jr., eds. *El Río Orinoco como ecosistema.* Caracas.
- Huber, O. 1992. Chimantá, escudo de Guayana, Venezuela. Oscar Todtmann, Caracas.
- Huber, O. 1993. Notas explicativas sobre el “Decreto de los Tepuyes.” *Pantepui* 5:35–42.
- Huber, O. and C. Alarcon. 1988. Mapa de la vegetación de Venezuela, con base en criterios fisiográfico-florísticos. 1:2,000,000. MARNR-Fundación BIOMA, Caracas.
- Huber, O. and J. J. Wurdack. 1984. History of botanical exploration in Territorio Federal Amazonas, Venezuela. *Smithsonian Contributions to Botany* No. 56. Washington, D. C.

- Im Thurn, E. F. and S. Oliver. 1887. The botany of the Roraima expedition of 1884: being notes on the plants observed; with a list of the species collected, and determinations of those that are new. Transactions of the Linnaean Society of London, Botany 2(16):249-300.
- Iribertegui, R. 1987. Amazonas: El hombre y el caucho. Ediciones del Vicariato Apostolico de Puerto Ayacucho. Monograph 4:1-357.
- Maguire, B. 1955. Cerro de la Neblina, Amazonas, Venezuela. A newly discovered sandstone mountain. Geographical Review 45:27-51.
- Maguire, B. 1970. On the flora of the Guayana Highlands. Biotropica 2:85-100.
- MARNR (Ministerio del Ambiente y de los Recursos Naturales Renovables). 1985. Atlas de la vegetación de Venezuela. Caracas.
- Mayr, E. and W. H. Phelps, Jr. 1967. The origin of the bird fauna of the south Venezuelan highlands. Bulletin of the American Museum of Natural History 136(5):269-328.
- Means, D. B. 1994. Venomous snakes of South America. South American Explorer 36:23-29.
- Means, D. B. 1995. Lost worlds, tepui natural history. (In preparation.)
- Mitsch, W. J. and J. G. Gosselink. 1993. Wetlands, 2nd ed. Van Nostrand Reinhold, New York.
- Myers, J. G. 1936. Savanna and forest vegetation of the interior Guiana plateau. Journal of Ecology 24: 162-184.
- Navid, D. 1989. The international law of migratory species: the Ramsar Convention. Natural Resources Journal 29:1001-1016.
- Nott, D. 1972. Angels Four. Prentice-Hall, Inc. 191 p.
- Priem, H. N. A., N. Boelrijk, E. Hebeda, E. Verdurmen, and R. Verschure. 1973. Age of the Precambrian Roraima Formation in northeastern South America: Evidence from isotopic dating of Roraima pyroclastic rocks in Surinam. Geological Society of America Bulletin 84:1677-1684.
- Rull, V. 1991. Contribucion a la paleoecologia de Pantepui y la Gran Sabana (Guayana Venezolana): clima, biogeografia y ecologia. Scientia Guaianae 2:1-133.
- Schomburgk, R. 1840. Journey from Fort San Joaquim, on the Rio Branco, to Roraima, and thence by the rivers Parima and Merewari to Esmeralda, on the Orinoco, in 1838-9. Journal of the Royal Geographical Society 10(2):191-247.
- Shaw, S. P. and C. G. Fredine. 1956. Wetlands of the United States, their extent, and their value for waterfowl and other wildlife. U.S. Department of Interior, Fish and Wildlife Service Circular 39. Washington, D. C. 67 p.
- Steyermark, J. A. 1982. Relationships of some Venezuelan forest refuges with lowland tropical floras. Pages 182-220 in G. T. Prance, ed. Biological diversification in the tropics. Columbia University Press, New York.
- Steyermark, J. A. 1986. Speciation and endemism in the flora of the Venezuelan tepuis. Pages 317-373 in F. Villeumier and M. Monasterio, eds. High altitude tropical biogeography. Oxford University Press.
- Tate, G. H. 1930. Notes on Mount Roraima region. Geographical Review 20:31-52.
- Tate, G. H. 1938. Auyantepui, Notes on the Phelps Venezuelan Expedition. Geographical Review 28: 452-474.
- Tate, G. H. and C. B. Hitchcock. 1930. The Cerro Duida region of Venezuela. Geographical Review 22: 31-52, 3 sketches, 16 photos, 1 map.
- Weibezahn, F. H. and B. E. Janssen-Weibezahn. 1990. El Territorio Federal Amazonas, Venezuela: una bibliografía. Scientia Guaianae, 1:1-294.
- Zoltai, S. C. and F. C. Pollet. 1983. Wetlands in Canada: their classification, distribution, and use. Pages 245-268 in A. J. P. Gore, ed. Mires: Swamp, bog, fen, and moor. Elsevier, Amsterdam.