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# Canopy dieback in lower montane forests of Alto Urimán, Venezuelan Guayana

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## Abstract

Canopy dieback in patches was discovered in an otherwise undisturbed very humid lower montane forest on a quartzitic sandstone plateau of the middle Caroní river basin, Venezuela. The patches vary in size from about 0.1 to 2 ha (50 to 700 upper story dead trees per ha). Preliminary inventories were carried out at 3 selected sites comparing 4 dieback patches (M) with adjacent not affected (V) forests. In the M plots, 40 to 61% of all trees with dbh $\geq$ 10 cm were dead. They consisted mostly (81–100%) of the endemic tree species *Terminalia quintalata* of the upper story (dbh $>$ 20 to 60 cm, height up to 30 m), which is much sparser in the V stands. Data on stand structure and species composition are presented. They seem to indicate a spatial variation in the density of *Terminalia quintalata*, but also of other dominant species, and reproductive problems of *Terminalia*, which is hardly present in the diameter classes below 10 cm dbh. V and M stands grow on similar soils with a perched high water table. They are practically free of clay and rich in humus. The exchange complex is dominated by $H^+$. Low pH and dilution of base cations represent the main chemical stress factors. Different concepts of the dieback process are discussed, including cyclic reproductive patterns, nutrient sequestering and drought frequency.

## Introduction

Canopy or stand-level dieback is a structural disturbance during which large groups of trees die for no obvious reason and remain standing upright (Mueller-Dombois 1991). The phenomenon is widespread in some Pacific forests that are not affected by environmental pollution or epidemic diseases. According to several studies, summarized in Mueller-Dombois (1986, 1988, 1991, 1992, 1995), the dieback phenomenon in the Pacific forests has been considered as natural and recurrent and is explained by the cohort senescense theory.

In some regions of southern Venezuela, canopy disturbances in various forms of tree groups or accelerated individual mortality appear to be quite frequent in the tropical moist forests (Fölster 1986, 1992, 1994; Hernández 1992; Dezzeo 1990, 1994). They are mostly regions with low human population, difficult access, low impact by human activities like shifting cultivation, mining and other sources of pollution. These forests survive under poor edaphic conditions by means of a closed nutrient cycle (Stark & Spratt 1977; Herrera et al. 1978; Jordan 1985; Medina & Cuevas 1989), and it has been demonstrated that under the impact of internal chemical and hydric stress and external events like severe droughts and fire, these forest ecosystems may be fragile and even unstable (Dezzeo 1994; Fölster 1994).

In the present paper, we want to introduce patch dieback phenomena in one of these regions, Alto Urimán, a forested plateau of about 420 km$^2$ in the middle part of the Caroní river basin. The patches have a size of about 0.1 to 2 ha, with 50 to 700 dead upper canopy trees per ha, and are well visible from low flying planes and on the air photos from 1968 (scale 1:50 000). They had been observed since the beginning of the last decade, and reported to the Corporación Venezolana de Guayana-Electrificación del Caroní (CVG-EDELCA), the state company responsible for the hydrological resources of the Caroní river basin.

Given that forest instability in the region could not only influence the global and regional carbon cycle but also the hydrology of the river basin, it has been decided to carry out a preliminary study of this phenomenon. This study has been logistically supported by CVG-EDELCA. The region is accessible only by helicopter, and even that access is restricted due to the frequent rains and cloud coverage of the plateau. Therefore, we could only carry out a limited number of field trips concentrating on inventories of vegetation and soils at 3 selected sites, where we did compare the dieback patches with the surrounding stands of low, regular mortality. On this basis, we have discussed the possible internal or external causes of the disturbance.

## Study area

The study area is located in the upper drainage of Río Urimán, an affluent of middle Caroní river basin, in SE Venezuela, between 05°20′–06°00′ N and 62°30′–63°00′ W, (Figure 1) at 600 to 1000 m asl. The bioclimate of the region can be classified as very humid premontane with mean annual precipitation above 3000 mm and a mean annual temperature between 21 °C and 24 °C (Holdridge 1947, adapted by Galán 1984). The closest meteorological station to our sites is that of Urimán village on the banks of Río Caroní (395 m asl) with 36 years of records (Figure 2). A mean of 4056 mm of annual precipitation is distributed unevenly. The wettest months are June and July with about 650 mm and a maximum of > 1200 mm. The driest months (January, February) normally receive > 60 mm, though this may be less in extremely dry years like 1964 (Figure 2).

The upper river basin of Río Urimán forms a large (420 km$^2$) slope-plateau set off from the surroundings at 3 sides by more or less pronounced escarpments, while the interior surface forms a slightly concave bowl reflecting the mild bending of the quartzitic sandstone which tops the strata of the Roraima Group, an assemblage of formations consisting of Precambrian rocks, with radiometric ages that range between 1600–1700 million years (Schubert et al. 1986). In a general sense (scale 1:250 000) the soils have been classified

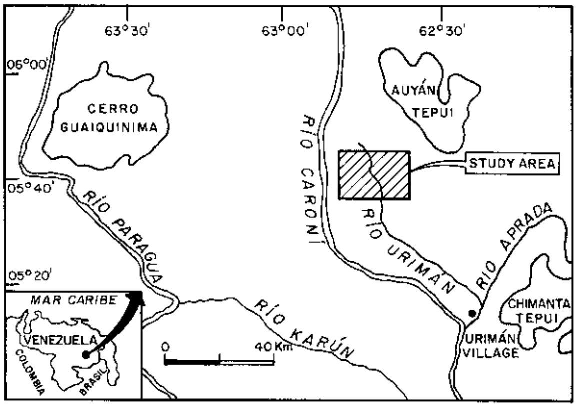

*Figure 1.* Location of the study area.

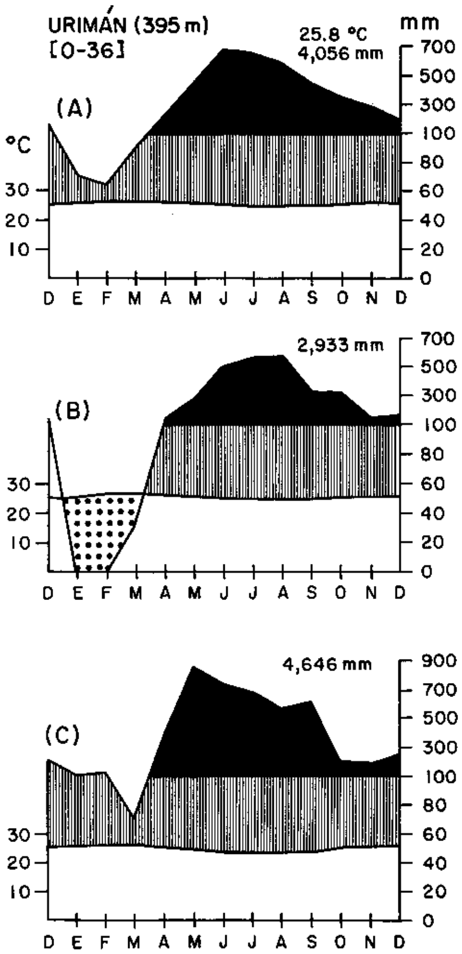

*Figure 2.* Climatic diagrams from Urimán following Walter (1979). (A): diagram of 36 years; (B): diagram of the driest year (1964); (C) diagram of the wettest year (1981).

according to the USDA classification system as Entisol (CVG-TECMIN 1989).

Phytogeographically, the region belongs to the Central Guayana Province of the Guayana Region (Huber 1994). The characteristic vegetation of the region has been defined by Huber & Alarcón (1988) and Huber (1995) as evergreen lower montane (submontane) forests (lower montane forest *sensu* Whitmore 1984). The actual vegetation cover consists of a mosaic of medium to tall (15–25 m) forests, low (8–12 m) forests, and shrublands. The size of the vegetation units varies from patchy islands to extensive uniform areas.

The patches of forest dieback with standing dead trees (Figure 3) occur as rounded islands in the higher forest and also as elongated zones bordering the low forest or shrub vegetation. The size of these patches may best be described as including several tens to more than 100 upper story trees easily visible from above (helicopter). All dieback patches, amounting to about 250 in an area of 80 km$^2$, are mainly restricted to the higher forest.

## Methods

Three sites were selected during helicopter surveys, firstly for the presence of medium forest with and without dieback and secondly for helicopter landing facilities (rock outcrops, low shrub vegetation nearby). At two sites we marked one and at one site two 400 m$^2$ plots in the dieback patch and in the unaffected medium forest respectively. Characteristics of the sites are:

- Urimán 1 (U1): Mosaic of shrubland, low and medium forest, at 950 m asl, with the two plots U1-M (dieback) and U1-V (without dieback) in close proximity. U1-M is surrounded by unaffected forest.
- Urimán 2 (U2): Mosaic of shrubland, low and medium forest, at 600 m asl, with the U21-M and U22-M (dieback plots) adjacent to U21-V and U22-V (unaffected forest). U21-M and U22-M are surrounded by unaffected forest.
- Urimán 3 (U3): continuous medium forest with dieback patches enclosed, at 850 m asl. The two plots U3-M (dieback) and U3-V (without dieback) are adjacent.

The size of the plots (10 × 40 m) does not satisfy normal vegetation survey standards but has been dictated by the restricted hours of helicopter access to the sites between events of heavy rains or low cloud cover. We still consider the plot size as justified for a first survey of the dieback phenomenon, as the differences between M- and V-plots become sufficiently clear. However, both plot size and number of sites need to be increased for a further understanding of the vegetation dynamics.

The stand survey includes recording of dbh, height and species for all trees with dbh $\geq$ 5 cm, and of smaller trees/plants on a subplot of 10 m$^2$ (1 × 10 m). Trees were identified with local names by our guide Paulisto Williams. Botanical samples were collected with and without reproductive organs for identification at the Herbario Nacional de Venezuela. Standing dead trees were identified using the criteria of the branch system of the crown and the stem bark. Some stem discs of live and dead trees of *Terminalia quintalata*, the dominant canopy tree, were collected for anatomic analysis.

Soils were sampled by auger in four depth intervals (0–20, 20–40, 40–60, and 60–80 cm) in the central part of the plots. Soil texture was determined by Bouyucos method (Day 1965), pH in $H_2O$ and 0.01 N $CaCl_2$ by glass electrode, C and N by dry combustion in CN Rapid Analyzer (Meiwes et al. 1984), and the exchangeable cations in $NH_4Cl$-extracts by atomic absorption spectrophotometry.

## Results

### *Structural data*

Table 1 presents the stand density, stand basal area and mortality of the healthy (V) and the dieback (M) stands. Mean tree density and basal area of all trees $\geq$ 10 cm dbh, both live and dead, are quite similar in the V plots (1125 trees ha$^{-1}$ and 39.1 m$^2$ ha$^{-1}$) and M plots (1113 trees ha$^{-1}$ and 48.2 m$^2$ ha$^1$), though the variability appears to be definitely greater in the M plots. The basal areas in the U22-M and U3-M plots can in fact be considered extraordinary large. Considering only the live trees, the differences between the V and M plots seem to be more pronounced in basal area (15 against 35 m$^2$ ha$^{-1}$) than in stem density (581 against 950 stems ha$^{-1}$). Dead trees make up 2 to 22% (1–16% of the basal area) in the V plots, but 40 to 61% (58–83% of the basal area) in the M plots.

This obvious discrepancy between tree density and basal area is explained in Table 2 by the different distribution of live and dead trees between diameter classes. While in the V plots, both live and dead

*Table 1.* Structural characteristics of the healthy (V) and the dieback (M) plots based on inventories of trees $\geq$ 10 cm DBH.

| Plots | | Stand density (trees ha$^{-1}$) | | | | Basal area (m$^2$ ha$^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Live trees | Dead trees | Total | % dead trees | Live trees | Dead trees | Total | % dead trees |
| Healthy stand | | | | | | | | | |
| U1-V | | 825 | 175 | 1000 | 17.5 | 34.0 | 4.0 | 38.0 | 10.5 |
| U21-V | | 950 | 275 | 1225 | 22.4 | 39.1 | 7.6 | 46.7 | 16.3 |
| U22-V | | 975 | 225 | 1200 | 18.8 | 31.1 | 4.7 | 35.8 | 13.1 |
| U3-V | | 1050 | 25 | 1075 | 2.3 | 35.4 | 0.3 | 35.7 | 0.8 |
| | * | 950 ± 94 | 175 ± 108 | 1125 ± 106 | 15.3 ± 8.9 | 34.9 ± 3.3 | 4.2 ± 3.0 | 39.1 ± 5.2 | 10.2 ± 6.7 |
| Dieback stand | | | | | | | | | |
| U1-M | | 800 | 525 | 1325 | 39.6 | 14.8 | 23.3 | 38.1 | 61.2 |
| U21-M | | 250 | 300 | 550 | 54.5 | 8.5 | 28.3 | 36.7 | 76.9 |
| U22-M | | 425 | 675 | 1100 | 61.4 | 8.7 | 42.7 | 51.4 | 83.0 |
| U3-M | | 850 | 625 | 1475 | 42.4 | 28.3 | 38.2 | 66.5 | 57.5 |
| | * | 581 ± 291 | 531 ± 166 | 1113 ± 405 | 49.5 ± 10.2 | 15.1 ± 9.3 | 33.1 ± 8.9 | 48.2 ± 13.9 | 69.7 ± 12.2 |

* Mean ± SD.

trees decrease in numbers from small to large diameters with an expected gradient, this gradient is almost lacking among the dead trees of the M plots, and only a few live trees exceed a dbh of 20 cm. This means that the dead trees in the dieback patches mainly occupy the upper story, while the live trees populate the small diameter class below 20 cm dbh and heights below 20 m (Figure 4). This difference between stories is a striking feature in the field, and strongly suggests the possibility of a secondary growth stimulation after the dieback event. The higher mean counts of life trees in the diameter class 5–10 cm of the M plots (Table 3) supports this interpretation.

Another important aspect in the M plots is that 81 to 100% of all dead trees (90% to 100% of their basal area) belong to the species *Terminalia quintalata* (Combretaceae). Few dead trees of this species are found among the dead trees of the V plots, but, except for U3-V, *Terminalia quintalata* does not contribute great numbers to the living trees of these stands (Figure 5). The dead *Terminalia quintalata* trees have the coarse branch system of the crown well preserved and also the stem bark appears little changed which facilitated their identification.

According to the botanical collections of *Terminalia quintalata* preserved in the National Herbarium of Venezuela (VEN), the Ovalles Herbarium in Caracas (MYF), and in the herbarium of the Missouri Botanical Garden (MO), one can conclude that this species is endemic in the submontane humid forests of the Guayana Shield between 400 and 1700 m asl. It can appear as a shrub, but its main life form is that of trees reaching up to 30 m and 50 cm dbh. Field observations seem to indicate that it is a gregarious species, which grows in groups in medium-high to low forests, as well as in shrublands. According to Maguire et al. (1957), *Terminalia quintalata* as also *Terminalia yapacana* show little similarity with any other species of the genus *Terminalia* of the New World.

Following the present appearance, forest stands of the dieback patches must have been greatly dominated by *Terminalia quintalata* in the upper stratum. Some trees survived in the dbh class $>$ 10 cm. In the class 5–10 cm dbh, young trees of this species still make up 12% in U1-M, and 2% in U21-M. In the remaining two M plots, no individuals of this species were registered (Table 3). This was also true in all V plots, and in all plots in the plant category $<$ 5 cm dbh. This category was abundant, especially in the M plots, and dominated by species of the Clusiaceae, Melastomataceae, Araliaceae, Rubiaceae, Myrtaceae, but also Arecaceae, Araceae, and Bromeliaceae. The latter plants can reach a high coverage in the ground flora, especially in the M plots. It seems from this evidence that *Terminalia quintalata* has problems of reproduction and regeneration.

### *Species composition and distribution*

The inventoried species in the study plots have been presented with their importance value in Table 4. It is important to state that the tree flora of the region is

*Figure 3*. Aerial view of the patch dieback phenomena in Alto Urimán. *Top*: a canopy dieback patch with adjacent non affected forest. *Bottom*: Mosaic of shrubland, low and medium forest, with many dieback patch (white) enclosed.

not yet well known, and only a few botanical samples could be collected with reproductive organs during the field work. Many species could only be identified to the genus or even family level.

*Table 2*. Number of trees per size class (cm DBH) in the healthy (V) and the dieback (M) stands based on inventories of trees $\geq$ 10 cm DBH.

| Plots | Live trees | | | | Dead trees | | | |
|---|---|---|---|---|---|---|---|---|
| | 10–20 cm | 20–30 cm | 30–40 cm | > 40 cm | 10–20 cm | 20–30 cm | 30–40 cm | > 40 cm |
| Healthy stand | | | | | | | | |
| U1-V | 475 | 275 | 0 | 75 | 150 | 25 | 0 | 0 |
| U21-V | 575 | 175 | 150 | 50 | 200 | 50 | 25 | 0 |
| U22-V | 675 | 250 | 0 | 50 | 175 | 50 | 0 | 0 |
| U3-V | 750 | 125 | 100 | 75 | 25 | 0 | 0 | 0 |
| * | 619 ± 120 | 206 ± 69 | 63 ± 75 | 63 ± 14 | 138 ± 78 | 31 ± 24 | 6 ± 13 | 0 |
| Dieback stand | | | | | | | | |
| U1-M | 725 | 25 | 50 | 0 | 175 | 300 | 25 | 25 |
| U21-M | 175 | 25 | 50 | 0 | 100 | 25 | 125 | 50 |
| U22-M | 375 | 25 | 25 | 0 | 250 | 175 | 175 | 75 |
| U3-M | 675 | 150 | 0 | 25 | 150 | 250 | 150 | 75 |
| * | 488 ± 259 | 56 ± 63 | 31 ± 24 | 6 ± 13 | 169 ± 63 | 188 ± 120 | 119 ± 66 | 56 ± 24 |

* Mean ± SD.

*Table 3*. Total number (ha$^{-1}$) of live and dead trees (5-10 cm DBH) of all inventoried species and percentage of live trees of *Terminalia quintalata* in the healthy (V) and the dieback (M) stands.

| Plots | Live trees | Dead trees | (%) dead trees | % live trees *T. quintalata* |
|---|---|---|---|---|
| Healthy stand | | | | |
| U1-V | 625 | 175 | 21.9 | 0.0 |
| U21-V | 650 | 50 | 7.1 | 0.0 |
| U22-V | 650 | 175 | 21.2 | 0.0 |
| U3-V | 1375 | 200 | 12.7 | 0.0 |
| * | 825 ± 366.8 | 150 ± 67.7 | 15.7 ± 7.1 | |
| Dieback stand | | | | |
| U1-M | 1025 | 250 | 19.6 | 12.2 |
| U21-M | 1100 | 150 | 12.0 | 2.3 |
| U22-M | 1650 | 50 | 2.9 | 0.0 |
| U3-M | 825 | 200 | 19.5 | 0.0 |
| * | 1150 ± 352.9 | 163 ± 85.4 | 13.5 ± 7.9 | 3.6 ± 5.8 |

* Mean ± SD.

The number of tree species (dbh $\geq$ 5 cm) that were inventoried in the healthy (V) plots range between 7 (U22-V) and 26 (U3-V) per 400 m$^2$. The range within the dieback (M) plots is much narrower (17–19). With such few plots, however, one cannot say whether this difference has any significance or is accidental. Counting the species on all V and M plots respectively, no difference can be found (37 versus 38 species per 1600 m$^2$).

Seventy five percent of all encountered species are found both in V as well as M situations, and the remaining 25% mostly belong to the rare species with low importance values. It seems reasonable, therefore, to assume little basic floristic differences. The picture changes when we consider only the more dominant species in the plots. All plots contain species with importance values $\geq$ 10% among the living trees. They may reach up to 73% of total density and up to 56% of basal area (Table 5). One can recognize in Table 5

*Table 4.* Inventoried species of live trees and shrubs (DBH $\geq$ 5 cm) in the healthy (V) and the dieback (M) stands and their relative importance (relative density + relative basal area /2).

| | Healthy stand | | | | Dieback stand | | | |
|---|---|---|---|---|---|---|---|---|
| Species | U1-V | U21-V | U22-V | U3-V | U1-M | U21-M | U22-M | U3-M |
| *Clusia* sp. | 26.1 | – | – | 0.6 | 5.0 | 1.2 | – | – |
| *Terminalia quintalata* | 15.6 | 4.3 | – | 32.7 | 11.4 | 11.9 | 5.9 | 6.3 |
| *Euterpe* sp. | 12.0 | – | – | 4.4 | 4.7 | 15.1 | 14.8 | 6.1 |
| Guttiferae | 8.8 | – | – | – | 5.3 | – | – | – |
| *Ladenbergia lambertiana* | 8.1 | – | – | 1.0 | 1.1 | – | – | 0.9 |
| *Protium* sp. | 5.0 | 7.8 | – | 1.6 | 1.8 | 10.6 | 8.1 | – |
| Icacinaceae | 6.0 | – | – | – | 3.7 | 1.4 | – | 1.8 |
| Apocynaceae | 3.8 | 1.6 | – | 4.2 | – | 9.1 | 2.0 | – |
| *Vochysia* sp. | 3.3 | 2.8 | – | – | – | – | – | – |
| *Pradosia schomburgkiana* | 3.2 | 1.1 | 1.2 | 10.6 | 8.1 | 7.0 | 18.7 | 16.3 |
| *Matayba* sp. | 2.2 | 1.7 | – | 0.7 | – | – | – | 0.9 |
| *Schefflera* sp. | 1.8 | – | – | 0.6 | – | – | 2.2 | 1.1 |
| *Pagamea capitata* | 1.2 | – | – | 0.7 | 24.9 | – | 15.4 | 2.0 |
| *Retiniphyllum* sp. | 1.0 | – | – | 2.5 | – | – | – | 3.5 |
| *Aspidosperma steyermarkii* | 1.0 | – | 1.5 | – | 1.8 | – | – | – |
| *Guatteria* sp. | 0.9 | – | – | – | – | – | – | – |
| Leguminosae 1 | – | 25.8 | 55.6 | – | – | – | – | – |
| *Caraipa tereticaulis* | – | 24.3 | 17.2 | – | – | – | – | – |
| *Dimorphandra macrostachya* | – | 12.1 | 13.0 | 0.8 | – | 11.0 | – | 1.7 |
| *Siparuna* sp. | – | 8.0 | – | 0.9 | 0.9 | – | – | 4.1 |
| Myrtaceae | – | 4.0 | 2.2 | – | – | 1.2 | 0.8 | – |
| *Catostemma* sp. | – | 2.7 | – | – | – | – | – | – |
| Leguminosae 2 | – | 1.8 | – | – | – | 2.5 | – | – |
| *Mauritiella* sp. | – | 1.1 | – | – | – | – | – | – |
| *Sloanea sp.* | – | 0.9 | – | 0.9 | 1.7 | – | – | 2.7 |
| Sapotaceae | – | – | – | 0.8 | 12.8 | – | 0.9 | 2.5 |
| Lecythidaceae | – | – | – | 1.6 | 6.3 | – | – | 3.3 |
| Sapindaceae | – | – | – | 2.8 | 2.4 | – | – | – |
| Leguminosae 3 | – | – | 9.3 | 1.5 | 1.1 | – | 0.8 | – |
| *Rudgea* sp. | – | – | – | 14.7 | – | 6.5 | 6.3 | 29.3 |
| Leguminosae 4 | – | – | – | 6.4 | – | – | – | 14.4 |
| Clusiaseae | – | – | – | 3.3 | – | – | – | – |
| *Cybianthus* sp. | – | – | – | 1.6 | – | 5.1 | 5.0 | – |
| Lauraceae | – | – | – | 1.6 | – | – | – | – |
| Myrtaceae | – | – | – | 1.5 | – | – | – | – |
| *Macrolobium* sp. | – | – | – | 1.4 | – | – | – | 1.2 |
| Palmae | – | – | – | 0.6 | – | – | – | 0.9 |
| Ochnaceae | – | – | – | – | 1,8 | 4.7 | – | – |
| *Gongylolepis benthamiana* | – | – | – | – | 1.4 | – | – | – |
| *Euceraea nitida* | – | – | – | – | – | 3.1 | 1.6 | – |
| Proteaceae | – | – | – | – | 3.8 | – | 1.7 | 1.0 |
| Melastomataceae | – | – | – | – | – | 1.3 | – | – |
| Rubiaceae | – | – | – | – | – | 1.2 | – | – |
| *Remijia* sp. | – | – | – | – | – | 7.1 | 11.0 | – |
| *Spathelia fruticosa* | – | – | – | – | – | – | 2.3 | – |
| *Miconia* sp. | – | – | – | – | – | – | 1.4 | – |
| *Pachira* sp. | – | – | – | – | – | – | 1.1 | – |

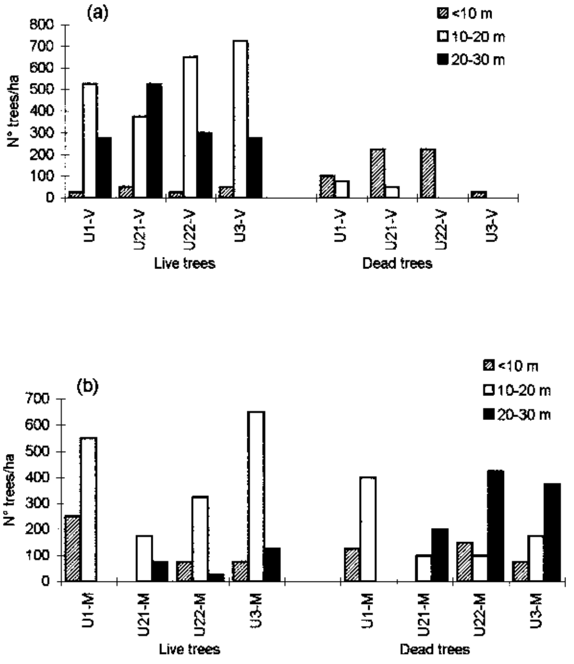

*Figure 4.* Number of live and dead trees with DBH $\geq$ 10 cm for height class in the healthy (a) and dieback (b) stands.

by comparing density and basal area that such dominance may occur in the lower but also in the upper strata. Some species turn up in different plots as dominants like *Dimorphandra macrostachya.*, *Euterpe* sp., *Terminalia quintalata* and *Caraipa tereticaulis*, while other species are more site specific. However, the number of plots is insufficient to find out whether species dominance could be specific to the V or in the M situation.

Special attention should be directed to *Terminalia quintalata* which, among the living trees, is present as dominant in 4 out of 8 plots (Table 5), though it reaches a very high percentage of the basal area only in U3-V (56%). In 3 plots this species concentrates in the upper stratum. Only in U1-M the figures of% total density and% basal area correspond to each other.

*Soil properties*

The soils on the quartzitic sandstone are shallow (60 to 100 cm) and sandy. The impervious rock below gives rise to a perched slope water table which – during the field work at the end of a period with less rain – was encountered at a depth of 40 to 80 cm. For most part of the year it can be expected to oscillate closer to the surface. In some instances, one could observe erosion rills which apparently were cut into the organic layer and the mineral soil when the water table rose above the surface and resulted in concentrated rill flow.

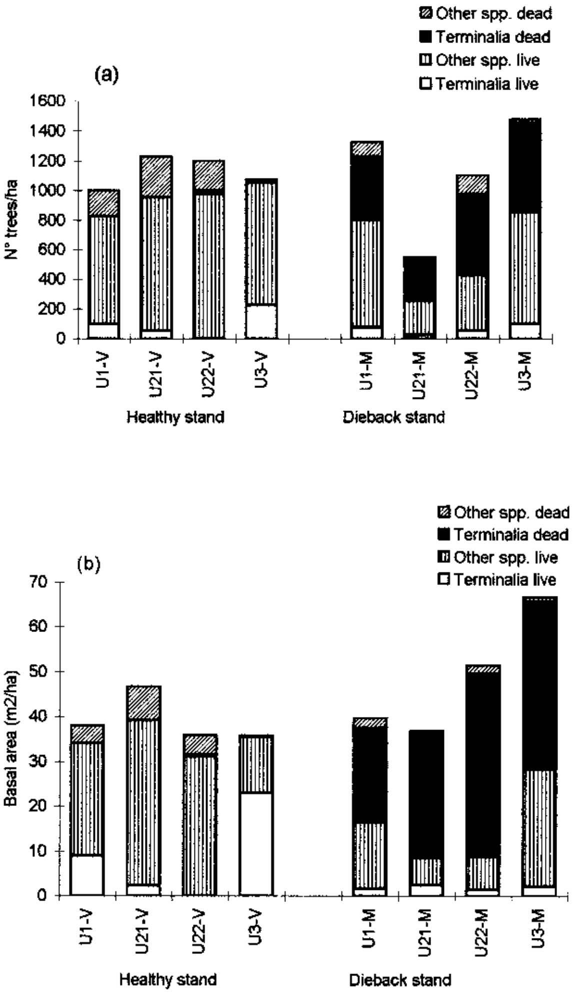

*Figure 5.* Density (a) and basal area (b) of live and dead trees ($\geq$ 10 cm BHD) of *Terminalia quintalata* and of the other species in the healthy and dieback stands.

Because of the virtual absence of silicates, including silicate clay minerals, the exchange functions are taken over by organic matter. The limited aluminum resources in the mineral soil keep exchangeable Al at very low concentrations ($<$ 5% of the effective cation exchange capacity -ECEC-). The exchange complex is dominated by $H^+$ (70 to 80% of the ECEC). The low pH (2.7–3.0) results from organic acids. No Al buffer interferes. If there is chemical stress in this system, it will not be caused by Al-toxicity but rather by the very low pH and the strong dilution of nutrient elements (Table 6).

*Table 5*. Percentage of the total density and the total basal area (live trees $\geq$ 5cm DBH) of the species with relative importance $\geq$ 10% in the healthy (V) and dieback (M) stand.

| Plot | Species | % of total density | % of total basal area |
|---|---|---|---|
| U1-V | *Clusia* sp. | 22.41 | 29.97 |
| | *Terminalia quintalata* | 6.90 | 24.27 |
| | *Euterpe* sp. | 20.69 | 3.39 |
| U21-V | Leguminosae 1 | 37.50 | 14.26 |
| | *Caraipa tereticaulis* | 17.19 | 31.43 |
| | *Dimorphandra macrostachya* | 4.69 | 19.45 |
| U22-V | Leguminosae 1 | 72.31 | 39.02 |
| | *Caraipa tereticaulis* | 10.77 | 23.51 |
| | *Dimorphandra macrostachya* | 4.62 | 21.33 |
| U3-V | *Terminalia quintalata* | 9.28 | 56.23 |
| | *Rudgea* sp. | 20.62 | 8.84 |
| | *Pradosia schomburgkiana* | 13.40 | 7.89 |
| U1-M | *Pagamea capitata* | 28.77 | 21.05 |
| | Sapotaceae | 2.74 | 22.80 |
| | *Terminalia quintalata* | 10.96 | 11.82 |
| U21-M | *Euterpe* sp. | 22.20 | 8.21 |
| | *Terminalia quintalata* | 3.70 | 20.26 |
| | *Dimorphandra machrostachya* | 3.70 | 18.26 |
| | *Protium* sp. | 12.96 | 8.19 |
| U22-M | *Pradosia schomburgkiana* | 9.64 | 28.07 |
| | *Pagamea capitata* | 16.84 | 14.19 |
| | *Euterpe* sp. | 20.48 | 9.08 |
| | *Remigia* sp. | 9.64 | 12,40 |
| U3-M | *Rudgea* sp. | 13.43 | 45.72 |
| | *Pradosia schomburgkiana* | 17.91 | 14.79 |
| | Leguminosae 3 | 14.93 | 13.80 |

Such conditions also retard microbial activity which leads to an accumulation of an organic surface layer and soil humus with a very wide C/N ratio (25–30). Humus readily infiltrates into greater depth of the mineral soil so that we find relatively high C-concentrations in the subsoil.

## Discussion

The inventories indicate that the submontane forests of Alto Urimán have a relatively high standing biomass considering the site quality. In terms of basal area (31–39 $m^2$ $ha^{-1}$), these forests can be compared with those studied by Hernández (1992) in the Gran Sabana in the Southeast (29–46 $m^2 ha^{-1}$), and those of the Duida–Marahuaca massif (Dezzeo & Huber 1995) in the South (16–46 $m^2$ $ha^{-1}$) of the study area. The event which caused the dieback in Alto Urimán considerably reduced the basal area of the living trees (58 to 83%) in the affected stands.

Between the dieback (M) and the non dieback (V) stands, no obvious site differences exist. Both stands are comparable in species composition, though most species have low importance value. Species with high importance value are in this position because of their basal area rather than their stand density. The most important difference apart from the mortality in M, is that *Terminalia quintalata* dominated M but is significantly less dominant (exception U3-V) in V.

Dominance of one or few species is relatively common in the humid tropical lowlands with high floristic diversity. In the Neotropics, one may list the forests dominated by *Carapa guianensis* in Costa Rica (Hall et al. 1994), the forests of *Mora gonggrijpii* and *Eperua falcata* in Guyana, and those of *Mora excelsa* in Trinidad (Richards 1966), the forests of *Perissocarpa* sp. and *Dimorphandra* sp. on the table mountain of Duida, Southern Venezuela (Dezzeo & Huber 1995), and those

*Table 6.* Soil properties in the dieback (M) and the healthy (V) stands.

| Plot | Depth | Clay | pH | C | N | C/N | $H^+$ | $K^+$ | $Ca^{++}$ | $Mg^{++}$ | $Al^{+++}$ | ECEC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | cm | % | $CaCl_2$ | % | % | | $\text{cmol}_c\ \text{kg}^{-1}$ | | | | | |
| | 0–20 | 3.1 | 2.80 | 4.14 | 0.14 | 29.6 | 2.100 | 0.071 | 0.190 | 0.135 | 0.133 | 2.74 |
| Dieback | 20–40 | 2.2 | 2.80 | 2.71 | 0.09 | 30.1 | 1.953 | 0.055 | 0.252 | 0.123 | 0.089 | 2.58 |
| stand: | 40–60 | 2.0 | 2.80 | 2.88 | 0.10 | 28.8 | 2.050 | 0.037 | 0.104 | 0.085 | 0.133 | 2.53 |
| U3-M | 60–80 | 1.8 | 2.88 | 1.65 | 0.06 | 27.5 | 1.321 | 0.028 | 0.088 | 0.058 | 0.089 | 1.70 |
| | $> 80$ * | | | | | | | | | | | |
| | 0–20 | 2.6 | 2.82 | 3.18 | 0.11 | 28.9 | 1.772 | 0.038 | 0.122 | 0.089 | 0.133 | 2.26 |
| Healthy | 20–40 | 2.6 | 2.90 | 2.09 | 0.07 | 29.8 | 1.531 | 0.035 | 0.136 | 0.082 | 0.000 | 1.89 |
| stand: | 40–60 | 2.4 | 2.92 | 1.37 | 0.05 | 27.4 | 1.256 | 0.028 | 0.088 | 0.051 | 0.311 | 1.83 |
| U3-V | 60–80 | 2.0 | 3.05 | 0.79 | 0.03 | 26.3 | 0.793 | 0.014 | 0.008 | 0.004 | 0.356 | 1.20 |
| | $> 80$ * | | | | | | | | | | | |
| Dieback | 0–20 | 2.4 | 2.92 | 2.40 | 0.10 | 25.2 | 1.512 | 0.118 | 0.180 | 0.165 | 0.111 | 2.25 |
| stand: | 20–40 | 2.0 | 2.90 | 2.30 | 0.09 | 25.5 | 1.924 | 0.090 | 0.240 | 0.145 | 0.178 | 2.74 |
| U21-M | $> 40$ * | | | | | | | | | | | |
| | 0–20 | 2.6 | 2.76 | 2.82 | 0.10 | 28.1 | 2.047 | 0.108 | 0.110 | 0.051 | 0.045 | 2.47 |
| Healthy | 20–40 | 2.4 | 2.80 | 2.25 | 0.08 | 28.1 | 1.513 | 0.063 | 0.060 | 0.145 | 0.000 | 1.91 |
| stand: | 40–50 | 2.4 | 2.70 | 2.16 | 0.08 | 27.0 | 1.512 | 0.048 | 0.060 | 0.142 | 0.089 | 1.98 |
| U21-V | $> 50$ * | | | | | | | | | | | |

* Water table.

of *Eperua purpurea* and *Monopterys uacu* (Franco & Dezzeo 1994) and of *Eperua leucantha* (Klinge & Herrera 1983) in San Carlos de Rio Negro, Southern Venezuela. Dieback phenomena of the type observed in Alto Urimán with *Terminalia quintalata* have not been recorded by Clark (1990) for the Neotropics, or by Pickett & White (1985) and Goldammer (1992) globally (see, however, Mueller-Dombois etc. below).

Looking for an explanation for the described phenomenon, one should consider the apparently group-like distribution of *Terminalia quintalata* and the poor regeneration ($<$ 10 cm dbh) below, together with the dieback. Though sparse but consistent regeneration might be a reproductive strategy of species, it can also indicate a heliotropic character. The fact that *Terminalia quintalata* is found also in shrubland (arbustal) of the Venezuelan Guayana (Huber 1995) may support this interpretation, though Hernández (1992) observed that many tree species of the region have no well defined light-shade disposition, i.e. they may function as pioneers but also form stable components in the upper story of multilayered primary forests.

Still, both the distribution and regeneration of *Terminalia quintalata* could suggest a type of cyclic reproduction (‘direct or auto-succession’) as has been described for *Metrosideros polymorpha* forests in Hawaii (Mueller-Dombois 1986, 1988, 1991, 1992, 1995; Auclair 1993) and those of *Scalesia pedunculata* on the Galapagos islands (Lawesson 1988; Mueller-Dombois 1988, 1991). *Metrosideros polymorpha* is a pioneer tree which grows up into a prolonged stage of maturity after which it finally enters senescence. Because of a lack of shade-tolerant canopy trees in these young island rain forests, the succession continues with the same dominant canopy species, but a shift in *Metrosideros* races from pubescent-leaved to glabrous-leaved forms has been documented (Drake and Mueller-Dombois 1993; Kitayama et al. 1995). After the stand collapses and a new pioneer stand usually grows up (called ‘replacement dieback’), or in some situations new species form the next canopy (called successional ‘displacement dieback’).

At a first glance, it appears that the Hawaiian concept might fit the observations in Alto Urimán. Instead of the phytogeographically determined lack of tree species that could lead to a succession of a primary mixed species forest on Hawaii, one might think of the marginal site conditions at Alto Urimán as cause for a strongly reduced number of shade-tolerant canopy species. But such species are apparently present in the unaffected stands. As little is known about the behavior and the reproductive biology of *Terminalia quintalata* and the other species, one cannot really pursue this analogy along this line.

Doubt concerning the applicability of the concept of ‘direct or auto-succession’ arises from the areal structure of the woody vegetation in Alto Urimán. If the Hawaiian concept applies, and forest dynamics would partly be governed by the senescence of the pioneer forest, one should encounter a patchwork of different stages of pioneer regrowth. In Alto Urimán, this is certainly not so. Apart from the islands of high forest, which include the dieback patches, there are islands and also extensive areas of shrubland to very low forest, but no intermediate stages towards higher forest. So, there must be other processes and determinants involved in the process.

Mueller-Dombois (1988), in a general paper on dieback phenomena, differentiated between predisposing factors (pollution, climatic changes, soil toxicity, nutrient imbalance, senescence), precipitating factors (periodically returning environmental stress like droughts or inundations), and accelerating influences (epidemic diseases, insect calamities). Based on above thoughts, one could also develop another concept for Alto Urimán:

The soils of Alto Urimán are developed from clay-free quartzitic sandstone without primary silicates, and are consequently free of exchangeable Al and Al toxicity. The lack of Al-buffer permits very low pH-values. We see the greatest chemical stress, however, in the strong dilution of nutrients which the root system has to capture from the horizontal saturated water flow, and the slow mineralization of the organic turnover. A limited store of nutrients, especially base cations, presents a crucial problem, and its stress impact increases the more as a growing biomass accumulates this limited resource and takes it out of the nutrient cycle. Our own observations in the Gran Sabana, SE-Venezuela, indicate (Dezzeo 1994) the probability that this process may lead to an autochthonous destabilization of forests with similar or different forms of dieback. We would consider this a predisposing factor.

A precipitating factor could be drought stress. Once the lateral seepage water is cut off from constant supply, it will rapidly drain off and leave the sandy soil with virtually no store of plant available water. The importance of this constant water supply can be supported by studies of Klinge & Herrera (1983) and Herrera (1977) considering the relation between the caatinga forest and the adjacent bana shrubland near San Carlos de Rio Negro in southern Venezuela. Both vegetation types coexist on quartz sand sediments in alluvial lowlands, the forests at sites with constant groundwater, the bana at sites with fluctuating water level. Pure quartz sands occur in other parts of the Venezuelan Guayana. Apart from the equally humid slopes of the Sierra de Lema, no forests are observed on these sites which have a regular dry season of 2–3 months.

Such dry seasons may exert minor impacts on the forest vegetation, the larger impacts can be expected in exceptionally dry years which will be more frequent in the drier than in the wetter regions. During the period of continuous weather records, such a dry year occurred during 1964 even in the more humid parts. 60 days were recorded without any rain at Urimán (Figure 2). The impact of such a year will certainly be more easily remedied in forests with less chemical stress than in forests with low resilience. On air photos from 1968, the dieback patchwork can already be recognized, apparently also in the present extension though with less clarity. The scale of the photos (1: 50 000) does not allow a more precise comparison with the patch structure of today.

Even if one accepts the feasibility of this interpretation, we still seem to be stuck with one problem: In Alto Urimán shrublands and very low forests seem to expand at the expense of the medium high primary forest. No intermediary regrowth stages have been observed. Why does a forest not grow up again after the external event and collapse? One reason suggested and quantitatively supported by Dezzeo (1994) for different pathways of destabilization SW of Urimán, was the loss of nutrients inflicted to the ecosystem during the disturbance, which practically prevents a restoration. This is seen as one cause of the savannization actually in progress in that region.

In the case of Alto Urimán one should, however, also be open to another line of thought. Long-term climatic change with decreasing humidity and/or increasing frequency of drought periods could also prevent the reestablishment of forests with higher biomass as a higher frequency of drought years reduce the resilience of the former ecosystem. We are inclined to give this thought some weight, as we have observed in other parts of the Venezuelan Guayana naturally occurring changes from forests with higher to forests with lower biomass (Dezzeo 1994). In this case, and under quite different site conditions, the process is connected with an increasing gap phase frequency.

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