A landscape ecological vegetation map of Sint Eustatius (Lesser Antilles)

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Abstract

A semi-detailed landscape-based vegetation map (scale: 1: 37,500) based on field data from 1999 has been available as an update of Stoffers' 1956 map of the Lesser Antillean island of St. Eustatius, Netherlands Caribbean, but up to now was never finalized or published. In this report we complete the documentation of that map to provide new insights into vegetation change over a period of more than 40 years, and a quantitative reference point for future studies on landscape-level vegetation development for the island.

The principal lower sections of the 21 km² island of St. Eustatius possess a tropical savannah climate according to the Köppen (1931) classification system, and the documented flora of the island amounts to 505 species. Color aerial photographs (1: 8,000) taken in 1991 and field data from 1999 were used to produce the map. A total of 84 vegetation sample plots were analysed using a stratified random sampling design and TWINSPAN cluster analysis.

Four main and 16 sub-landscape types were distinguished based on geology, geomorphology and different mixes and expressions of the component vegetation types. The five principal landscape types are in descending order of importance: H1, H2, M4, M9 and C, and covered some 67 % of the seminatural habitat of the island. H1 and H2 are the *Pisonia-Justicia* hills and *Pisonia-Bothriochloa* hills and are limited to The Mountains area. Analysis of the sampling data resulted in the distinction of 13 (semi)natural vegetation types. The three principal vegetation types were, the *Pisonia-Justicia* type, *Pisonia-Ayenia* type and *Bothriochloa-Bouteloua* type which together accounted for 38 % of total (semi)natural vegetation cover. The following well-developed vegetation types of St. Eustatius represent primary climax communities: Types 1, 2, 3, 5 and 7, all found in and around the Quill in the southwestern part of the island. A comparison of the vegetation types in the present study with those of Stoffers (1956) showed that only one vegetation type closely resembles one in Stoffers' study. Major changes have taken place in certain types of the natural vegetation of the island in the intervening five decades.

The majority of the central sections of the island around Oranjestad the so-named "Cultuurvlakte", amounting to approximately 25 % of the surface of the island, have suffered intensive disturbance due to past agriculture, livestock husbandry and invasive species and were not mapped. Only a small remnant portion of the semi-natural lowlands vegetation (L1 and L2) was left in the coastal reaches of Billy's Gut. Nevertheless, this area is heavily affected by grazing and the invasive vine *Antigonon leptopus*.

A comparison with the 1950s vegetation map by Stoffers shows that the rarest and most valuable elfin woodland vegetation of the rim of the Quill crater had been largely lost and that the areas he described as "Montane thickets" (Type 2) had declined and been degraded. We speculate that these losses may be most directly attributable to the impact of recent hurricanes and/or grazing by introduced livestock. On the lower slopes of the Quill, several areas mapped by Stoffers as farmland had been abandoned and have evidently regenerated into mixed deciduous and evergreen thorny woodlands.

The vegetation of the Mountains area showed some recovery since the 1950s. There were more evergreen bushes, and less *Acacia* and *Leucaena* than Stoffers described. The vegetation Stoffers described for the lowlands had more *Acacia* than we found but the invasive *Antigonon* has since dramatically increased as a ubiquitous and often dominant species. The former importance of *Opuntia* prickly pear cacti in disturbed vegetations has dramatically declined since the 1950s. We ascribe this to the likely effect of the invasive parasitic insect *Cactoblastis cactorum*. In the 1980s and 1990s many *Opuntia* cacti were seen affected by this insect (G. Lopes, pers. comm.).

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Our field data show that all wilderness areas of St. Eustatius remained heavily affected by grazers. This reduces the resilience of natural vegetations and interferes with natural succession by imparting heavy losses to hardwood seedlings and saplings (see e.g. Melendez-Ackerman *et al.* 2008), by reducing plant biomass (which increases exposure to wind and sun), and by favoring hardy invasive plant species. In Curaçao, large scale reduction in densities of feral grazers in the Christoffelpark since 1993 has led to rapid recovery of several rare plant species and vegetation types. The problem of feral livestock remains severe. Therefore the number one priority for terrestrial conservation in St. Eustatius will be to reduce feral grazer densities and impacts in key wilderness areas.

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1 Introduction

The Dutch Caribbean volcanic island of St. Eustatius has a surface area of some 21 km² and lies between Saba (to the northeast) and St. Kitts (to the south-west) in the Lesser Antilles of the north-eastern Caribbean. The flora and vegetation of the island have been studied quite extensively (Boldingh 1909, 1913, 1914; Arnoldo 1964, 1967; Stoffers 1963-1984, 1981; Howard 1974-1989), but an up-to-date vegetation map remained critically lacking for conservation and land-use planning purposes.

Boldingh (1909) described the vegetation of the three Dutch Windward Islands (St. Eustatius, Saba and St. Maarten) only in general terms as 'that of a tropical zone without any pronounced dry season'. According to him, determinant factors affecting the state of vegetation development were the persistent wind, the presence or lack of humus in the soil, the high extent of deforestation and the many introduced species.

Stoffers (1956) was the first to provide a vegetation map for St. Eustatius, in which 18 vegetation types were described. His map was a low resolution map (scale ca. 1:37.000) based on limited qualitative observations and the classification system developed by Beard (1944, 1949, 1955). Until now only Stoffers' qualitative map and vegetation descriptions have been generally available. Land-use planning in the Dutch Caribbean began in the early 1980s and the need arose for up-to-date quantitative vegetation maps for all islands. After vegetation map projects for Curacao (Beers *et al.* 1997) and Bonaire (Freitas *et al.* 2005) we here provide a landscape ecological vegetation map for St. Eustatius using identical methods. These are based on aerial photo-interpretation and stratified quantitative sampling, and involved 84 sample plots distributed around the island (Zonneveld 1979, 1988a,b). Albeit on a rough scale, Stoffers' earlier work offered a unique opportunity and valuable tool with which to compare and assess developments in vegetation over a number of decades during which major changes took place in land-use practices. Among these are the virtual demise of agricultural cultivation, habitat loss for industrial development, and the rapid rise of invasive species.

In this report we finalize the presentation of the results of a (semi-)quantitative vegetation survey of St. Eustatius, including the description of terrain characteristics, vegetation structure, species composition and spatial patterns in the landscape, which has been available but unfinalized as based on field results from 1999. While in the most recent years some changes will have taken place in the detailed species composition of the vegetation units described, our results provide a major update compared to Stoffers' vegetation description and a quantitative reference point for future studies on vegetation development for the island.

The semi-detailed scale (Loth 1990) for the landscape ecological vegetation map of St. Eustatius is 1:37.500. Its units are delineated and characterized on the basis of landscape-forming factors, such as geology, geomorphology, soil characteristics and vegetation. The quantitative approach used will give the possibility to track changes in the vegetation types and their presence in landscape units over time. A comparison between islands is also possible because of the fact that landscape ecological vegetation maps will also be produced for the other two Windward Islands (Saba and St. Maarten) using the same methodology.

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2 The Island of Sint Eustatius

2.1 Geography

The volcanic island of St. Eustatius forms part of the inner arc of the Lesser Antilles (Stoffers 1956). The presence of Tertiary, Quaternary or (rarely) recent volcanoes is characteristic for these inner arc islands. St. Eustatius is situated between 17°28′ and 17°32′ N latitude and between 62°56′ and 63°0′ W longitude. The island has a surface area of about 21 km². The greatest length and greatest width of the island are resp. 8 km and 3.75 km. The Quill is a dormant Strato Volcano that has not erupted for more than about 1600 years (Mid-Holocene) and is the highest point of the island (600 m)(Roobol & Smith 2004). In the early 1980s the population of the island was about 2100 persons (De Palm 1985) and by the late 1990s approximately 2200 persons.

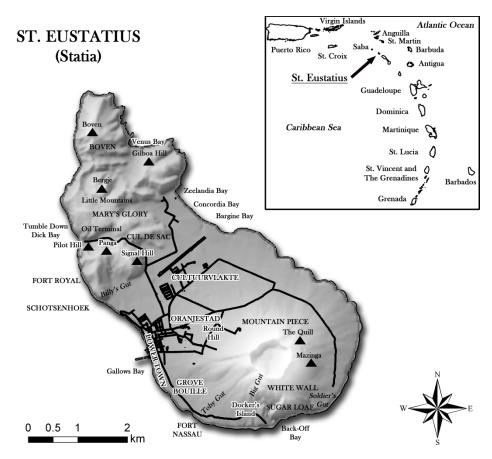


Figure 1 Map of the island of St. Eustatius with main topographical features, site names used in the text and the location of the island in the Lesser Antilles.

2.2 Climatic data

The annual average rainfall on St. Eustatius is 986 mm (1971-2000; Meteorological Service of the Netherlands Antilles & Aruba; Appendix 2). This is (approximately 10%) lower than the averages given by Stoffers (1956): 1110.6 mm (1947-1952; Meteorological Service of the Netherlands Antilles & Aruba) and 1089 mm (1881-1933; Braak 1935). However, rainfall can be quite variable. In the years 1997 and 1998 respectively 1302 mm and 1314 mm of rainfall were measured, 32% and 33% above the long year average for 1971-2000 (985.8 mm). According to Veenenbos (1955) the amount of rainfall on the Quill

(above 400 m) averages 1500-2000 mm per year. Unfortunately no rain stations are installed above 400 m so this cannot be confirmed by quantitative data.

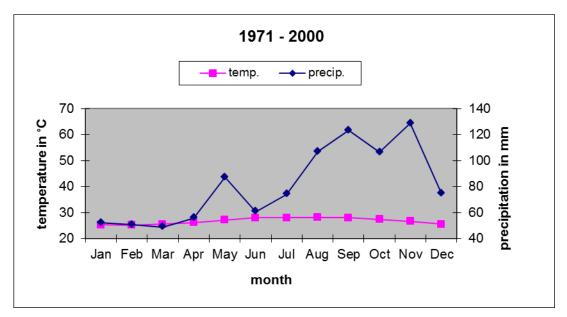


Figure 2 Walter climate diagram for the island of St. Eustatius (period 1971-2000; courtesy of: Meteorological Department Curação)

In general rainfall on the island is seasonal, with the months of August, September, October and November accounting for 47% of the long-term annual average (App. 3). This pattern was also the case during the period 1881-1933. Fig. 2 shows the climate diagram for St. Eustatius for the period 1971-2000. From the this it can be concluded that the dry period of the year is formed by the first four months of the year. In the months of August, September, October and November the average monthly rainfall is above 100 mm, the critical point below which evaporation exceeds precipitation in tropical areas (Beard 1949, Nix 1983).

The average minimum temperature on St. Eustatius varies between 22.3 °C and 25.0 °C (1971-2000; Meteorological Service of the Netherlands Antilles & Aruba; App. 3). According to the Köppen (1931) system of climate classification, the tropical climate of St. Eustatius falls in the A-category because the mean temperature of the coldest month exceeds 18°C (Augustinus *et al.* 1985). A further classification of the A-category can be reached using the amount and distribution of the precipitation:

Af: tropical rainforest climate with at least 60 mm precipitation every month;

Am: tropical monsoon climate with a short dry season and the driest month with rainfall less than 60 mm;

Aw: tropical savannah climate with a pronounced dry season, with the driest month having precipitation less than 60 mm.

According to Veenenbos (1955) the climate of St. Eustatius lies somewhere Am and Aw. The lower part of St. Eustatius (below 400 m) has an Aw-climate. With increasing altitude, the Aw-climate gradually changes into an Am-climate, because of increasing precipitation. It is even possible that at the top of the Quill an Af-climate occurs, though less moist in comparison to the Mount Scenery on Saba (Augustinus *et al.* 1985).

St. Eustatius is situated in the zone of the north-eastern trade winds. The most frequently occurring wind directions are NE, ENE and E; together they account for 80% of the wind direction frequency (Verstappen *et al.* 1972 in Augustinus *et al.* 1985). The average wind speed at 10 m height is 4.8 m/s (Appendix 2).

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St. Eustatius is located within the hurricane belt. The "official" Atlantic hurricane season extends from June 1 through November 30. Almost every year at least one hurricane passes within a range of 100 miles and on the average once every 4-5 years hurricane conditions are experienced (Meteorological Service of the Netherlands Antilles & Aruba 2010; and Appendix 3). Hurricanes that have caused significant damage to the nature of St. Eustatius more recently include Hugo (1989), Marilyn (1995), Georges (1998) and José and Lenny (1999). For nearby Saba, Nielsen (2007), points out that in the 50 year period up to Hugo in 1989, only two major hurricanes had affected the islands.

The average air temperature on St. Eustatius is 26.9° C (1971-2000;). In 1997 and 1998 the average temperature was respectively 26.5° C and 27.0° C. June (27.9 °C), July (28.0 °C), August (28.1 °C) and September (27.9 °C) are the hottest months, while February (25.2 °C) and January (25.3 °C) are the coldest.

2.3 Geology and geomorphology

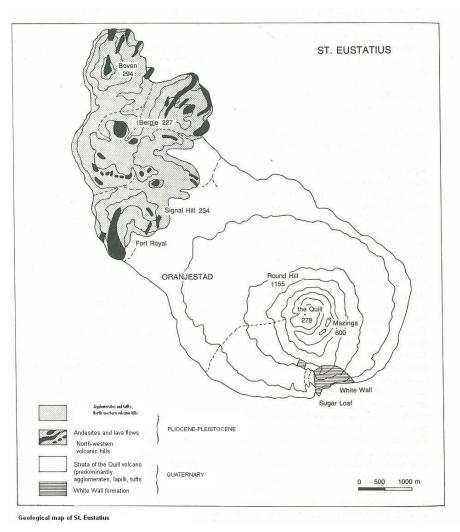


Figure 3 Schematic geological map of St. Eustatius (adapted from De Palm 1985).

2.3.1 Geology

Together with St. Kitts and Nevis, St. Eustatius lies on a shallow submarine plateau of maximally 180 m depth (Westermann & Kiel 1961).

St. Eustatius consists of three main geological units (Westermann & Kiel 1961):

- 1. North-western volcanic hills;
- 2. Quill volcano:
- White Wall formation.

1. North-western volcanic hills

These hills have a maximum height of 200-300 m and are the asymmetric remnant of one large strato volcano, whose crater was situated above the present hill of Bergje (223 m) (Westermann & Kiel 1961). The original crater may have reached a height of 610 m a.s.l. The first eruptions of this volcano date from probably the late Pliocene (16 million - 1 million years ago). It is presumed that the volcanic activity stopped in the early Pleistocene (approx. 2.5 - 0.8 million years ago). The original volcano has been strongly affected by erosion and denudation. Therefore, only the more solid parts have been preserved. Bergje is composed largely of pyroxene-andesites and to a lesser extent of agglomeratic deposits. Boven (289 m) and Gilboa Hill (175 m) are presumed to be solidified lava flows which have descended from the former central crater (Westermann & Kiel 1961). They both consist of andesites. The horseshoe shaped hill complex of Signal Hill - Cull de Sac - Panga - Pilot Hill is the remnant of the southern foot of the volcano. Several structures can be found in this part of the island, varying from ejactamenta to agglomerates, tuffs and lava (pyroxene-andesite and basltic pyroxene-andesite) (Westermann & Kiel 1961).

2. Quill volcano

The Quill volcano is a dormant strato volcano (Roobol & Smith 2004) with a symmetrical, regular truncated cone that evolved in the Holocene (10,000 years ago - present) (Westermann & Kiel 1961). The top, the crater and the foot of the volcano are all built up of loose material, representing the ejactamenta stage. The majority of rocks outcropping on the rim and the huge blocks lying on the bottom of the crater are predominantly pyroxene-andesites and basaltic pyroxene-andesite. Besides these types also andesitic tuffs and andesitic agglomerates are found in the crater of the Quill. Downwards on the slopes the ejactamenta become progressively finer. Tuff layers occur on the "Cultuurvlakte" and in the hilly north-west region. They are built up of volcanic ash, bombs ¹, lapilli ² and pumice ³. Due to the north-eastern trade winds, the finer material was blown in western directions. As a consequence, deposits found on the western flank of the volcano are finer than those on the northern, eastern and southern flanks. The crater of the Quill has not been badly affected by erosion and this is considered to indicate a relatively recent cessation of volcanic activity (Westermann & Kiel 1961). It is estimated that the latest phase of active volcanism took place about 8000 to 7500 years ago (Augustinus *et al.* 1985).

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¹ A bomb is a fragment of molten or semi-molten rock, 2 1/2 inches to many feet in diameter, which is blown out during an eruption. Because of their plastic condition, bombs are often modified in shape during their flight or upon impact.

 $^{^2}$ Literally, "little stones." Round to angular rock fragments, measuring 1/10 inch to 2 1/2 inches in diameter, which may be ejected in either a solid or molten state.

 $^{^3}$ Light-colored, frothy volcanic rock, usually of dacite or rhyolite composition, formed by the expansion of gas in erupting lava. Commonly seen as lumps or fragments of pea-size and larger, but can also occur abundantly as ash-sized particles.

The slopes of the Quill are characterized by two irregularities: the Round Hill and the White Wall complex (see next paragraph). The Round Hill (155 m) is a small, slightly arched, semi-spherical cone (probably a small additional crater or a lava dome) on the north-western slope of the Quill and of which the underlying rocks are completely covered by tuffs and debris. The north-western slope of Round Hill is much steeper than the south-eastern slope (Augustinus *et al.* 1985).

3. White Wall formation

On the southern side of St. Eustatius the regular form of the Quill is interrupted by the so-called White Wall and Sugar Loaf. Both consist predominantly of limestone either developed in a shallow, tropical sea bordering the partly denuded volcano, or in or near a lagoon surrounded by coral reefs (70,000 - 21,000 BP). The strata contain volcanic rock fragments and angular mineral fragments which have been ejected during initial submarine volcanism of the Quill. The stratigraphic thickness of White Wall is estimated at 150 m, whereas the Sugar Loaf stratum is estimated to be 50 m thick. The White Wall and Sugar Loaf complex was uplifted and tilted by the rise of a volcanic plug or dome, presumably in the middle of the Holocene. During later eruptions of the volcano, the White Wall was covered with some volcanic sand and ash from 130 m a.s.l. upwards (Westermann & Kiel 1961).

2.3.2 Geomorphology

St. Eustatius can be geomorphologically divided into three different main units (Augustinus et al. 1985):

- 1. The north-western hills;
- 2. The Quill;
- 3. The "Cultuurvlakte".

1. North-western hills

The relief of this part of the island is rather irregular and can be characterized as strongly dissected (Augustinus *et al.* 1985). There is a large range in slope angle ($0^{\circ} - >45^{\circ}$), caused by the differences in resistance of the geological formations to erosional forces. This can be recognized by the fact that generally the andesite outcrops have steeper slopes than the agglomerate and tuff deposits. Along the coast however the slopes are independent of the geological formations and reach angles of more than 28° .

Two major valley systems that reach the sea occur in the north-western hills: Venus Bay Valley and Tumble Down Dick Valley. They are considered to be "intermittent" valley systems because they only discharge water during and shortly after periods of heavy rainfall (Westermann & Kiel 1961).

In this region there is a marked difference between the western and eastern coastline in the sense that the western coastline is rather smooth compared to the eastern one which is characterized by an alteration of bays. These bays are built up of agglomerates and tuffs and promontories of the more resistant old lava flows. The differences in lithology are thus reflected in the morphology of this landscape.

2. Quill

The regularly shaped strato volcano on the southern part of the island reaches a height of 600 m at the eastern side of the rim, whereas it is only 378 m high on the western side. The width of the crater is about 750 m and the bottom lies at 273 m a.s.l. At an altitude of 150-200 m a.s.l. there is a marked change in slope angle. Above this height the slopes have angles of 30°-35°, whereas below this height the slope angle decreases rather abruptly to values between 15°-20°. This change coincides with the transition of volcanic materials from lapilli into fine tuffs.

The guts (ravine systems) on the southern and south-western part of the Quill only discharge water after heavy precipitation. Two examples of these ravines are Big Gut and Soldier's Gut, bordering the White Wall formation, at respectively the western and eastern side.

3. <u>"Cultuurvlakte"</u>

The "Cultuurvlakte" is morphogenetically the nearly flat footplain of the Quill volcano. The altitude above sea level ranges from 10 m to about 80 m, averaging 40 m (Augustinus *et al.* 1985). At the sea side, steep cliffs of 20-45 m high are present. An exception to this occurs at two places: on the leeward coast near Billy's Gut and on the windward coast in the northern part of Concordia Bay, where the plain merges into sandy beaches.

2.4 Soil- and landtypes of the geological formations

Due to the fairly dry sub-humid climate, soil formation is relatively very poor on St. Eustatius (Veenenbos 1955). For the description of the soils, the same division is used as applied to the geomorphological description (Augustinus *et al.* 1985; see Fig. 4):

- 1. The soils of the north-western hills;
- 2. The soils of the Quill;
- 3. The soils of the "Cultuurvlakte".

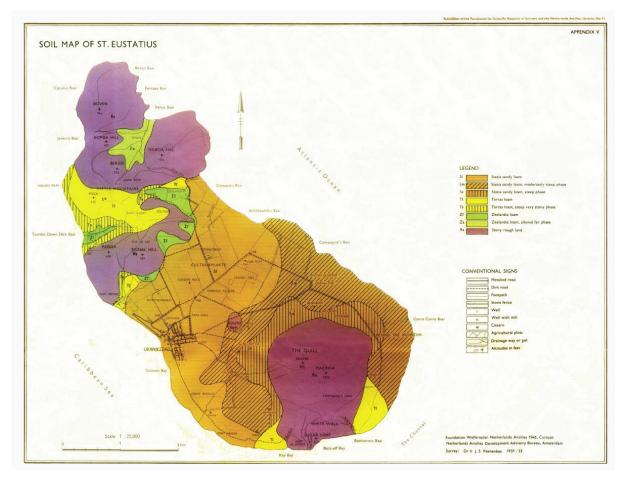


Figure 4 Soil map of St. Eustatius (source: Veenenbos 1955).

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1. The soils of the north-western hills

The main units distinguished by Veenenbos (1955) in this area are the 'Stony rough land' and the 'Terras loam'. Occasionally the 'Zeelandia loam' is also found (at e.g. Zeelandia and Venus bay). In this northern part of the island, the clay loam soils are very shallow, gritty, and stony. 'Zeelandia loam' occupies nearly level or gently sloping areas at the basis of hilly areas (slope gradient 1-10 %) and is derived from colluvial deposits, partly of the 'Terras loam' soils, and partly of weathered rock material. It is characterized by a 12-16 inch deep, very dark grey-brown to very dark brown, neutral, loamy surface soil. The structure resembles either that of the soft topsoil of the sandy loam soils, or is hard and very plastic when wet. The sub-soil consists of 6-8 inches deep, mostly very compact and very firm, neutral, very dark, grey-brown loam, rich in small grit in the process of weathering. In valley-like positions (e.g. at Zeelandia) these soils may be somewhat stony. The substratum consists either of the white, occasionally cemented buff, or of brownish grayish pumice. Drainage conditions are not favorable, owing to the slow internal drainage (Veenenbos 1955)

'Terras loam' is developed over soft white finely grained tuff. It generally occurs on land having slopes of 10-20 % (Veenenbos 1955). 'Terras' is the Caribbean name for this kind of volcanic ash. Characteristic for the 'Terras loam' is that it hardens readily when exposed to atmospheric influences and this is encountered directly under the surface soil. The soils derived from this parent material show the same cementation immediately under the surface. It is characterized by a 10-18 inches thick very hard, semi-granular or cloddy, neutral, brown to grey-brown, loam surface soil, apparently having a bulk density, and plastic when wet. Via a lighter colored transition zone of 4-6 inches, the topsoil grades into the whitish parent material which is cemented over a depth of about one foot. These soils are moderately well or well drained, because of the slope. Internal drainage is slow or very slow. Sheet erosion is severe; in areas with slopes over 20 % nearly all of the original surface soil has gone. At places (e.g. Pilot Hill, Fort Royal) the very stony phase of the 'Terras loam' can be found. This phase occurs in narrow valleys on slopes of more than 45 %. Most of these soils are very stony. These soils may be rather deep where colluvial accumulation has taken place between the stones (Veenenbos 1955).

On the andesites of these hills no more than a shallow, very steady topsoil overlies hard bedrock, partly on the account of the hardness of the parent material, and partly because of severe erosion. A certain amount of clay accumulation is observed in colluvial deposits at the foot of the slopes, between stones. The loamy soils of Mary's Glory and the bottom of Tumble Down Dick Valley which developed over soft, fine-grained tuff form an exception to these soils. The parent material is less hard and solid, and consists mainly of ash deposits of the Quill volcano, but even here soil formation is not very pronounced (Veenenbos 1955).

2. The soils of the Quill

In the crater and on the crater rim also the 'Stony rough land' occurs. There it is represented by coarse sandy loam soils. In general, these soils with slopes of over 45 degrees are very stony. At the middle-elevations of the Quill the 'Stony rough land' is succeeded by the 'Statia sandy loam, steep phase'. These soils differ from the typical soil ('Statia sandy loam') both in slope, stoniness, and structure of the surface soil. In general, they have a slope-gradient of 20-65 % and are very stony. The surface soil shows a crumb structure, which becomes more marked with increasing altitude. They also have higher organic matter content, increasing with height and reaching 8-10 % or more. The texture is the same as that of the typical soil. Stoniness increases with altitude and the soils are very susceptible to erosion. The moisture conditions are better than in the basic soil type of this group (Veenenbos 1955).

The 'Statia sandy loam, steep phase' is succeeded by a relatively broader area consisting of 'Statia sandy loam, moderately steep phase'. This phase has slopes of 10-30 % and has a stony or sometimes very

stony character. For the rest, this phase has the same characteristics as the basic soil type of this group (Veenenbos 1955).

In the south (Fort Nassau, Grove Bouille) the 'Statia sandy loam, moderately steep phase' is succeeded by the typical 'Statia sandy loam' that is found on the Cultuurvlakte. This soil is derived from andesitic pumice and occurs on the lower part of the glacis of the volcano on gently to moderately sloping land (5-16 %). In general there is a 10-18 inch deep, dark gray-brown to very dark grey-brown, loose, sandy loam surface soil, merging rapidly into the yellow-colored top layers of the grey parent material. The yellowish transition layer is usually 4-8 inches. The depth of the surface soil varies from a few inches to over 3 feet, depending on erosion. Formerly, gullies were formed which are now filled up for the greater part with topsoil material from elsewhere. The slightly acidic to neutral surface soil has a clay percentage of about 12-14. It is very dark, grey-brown, sandy loam soil, which has an organic matter content of about 5-7% in non-eroded places or places of accumulation. These soils are rather excessively drained on account of the porosity of the parent material. In dry periods the surface soil is loose and dusty. Shortly, after rainy periods, however, it seems to have a rather extensive water holding capacity, giving it a slippery character and a tendency to flow. In places, these soils maybe rather stony. Big bombs which are embedded in the pumice may lie at the surface (Veenenbos 1955).

In the southern part (to the west of Toby Gut and to the east of Soldier's Gut) the Stony rough land is succeeded by the 'Terras loam' (described above).

The soils on the lower parts of the concave slopes of the Quill have a rather good structure and are of a high quality, whereas the soils on the higher and steeper slopes are stony and are of poor quality. Most of the soils surrounding the Quill are of the Statia complex and developed over pumice (Veenenbos 1955). They have a loose, dusty, black surface. The grey pumice parent material is weathered over a few inches. On the higher slopes, with more rainfall and more favorable moisture conditions, this yellow weathering goes as deep as three feet/one meter. These Statia sandy loam soils, having an organic matter of 5-7 %, are the best of St. Eustatius, although they appear to be stony on the slopes of the Quill and thus hinder mechanical cultivation compared to the soils in the "Cultuurvlakte". On the more southern slopes of the Quill a loamy soil can be found (Veenenbos 1955).

According to Augustinus *et al.* (1985) two different soil types occur on the slopes of the Quill: Inceptisols and Mollisols. Their occurrence is largely determined by climatic conditions, which in turn are influenced by altitude. The Inceptisols are found between ± 300 m and ± 600 m a.s.l.. They are more or less freely drained. Higher on the slopes of the Quill (above 450 m) some pyroclastic materials can be found in these soils. Mollisols occur on the lower parts of the slopes, below ± 300 m a.s.l.. The soils are more or less freely drained and have a surface horizon rich in bases (i.e. the percentage of the soil exchange sites occupied by basic cations, such as potassium (K), magnesium (Mg), calcium (Ca), and sodium (Na) is high).

The soils of White Wall and Sugar Loaf are considered as a sub-group within the Quill soils. They have a higher pH, because of the marine origin of their parent material (Augustinus *et al.* 1985).

3. The soils of the "Cultuurvlakte"

This area is occupied by the 'Statia sandy loam'. The other two phases ('Statia sandy loam, moderately steep phase' and 'Statia sandy loam, steep phase') are derived from this soil type. This soil is derived from andesitic pumice and occurs also on the lower part of the glacis of the Quill volcano on gently to moderately sloping land (5-16 %). For a further description of the characteristics of this soil type therefore one is referred to the former paragraph ('The soils of the Quill').

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2.4.1 Flora and vegetation

The flora and vegetation of St. Eustatius have been studied quite extensively, although the information is quite dispersed over a number of publications (Boldingh 1909, 1913, 1914; Arnoldo 1971; Stoffers 1963-1984, 1981; Howard 1974-1989; and Wiersma 1984). More recently studies of the flora of the island have been conducted by the New York Botanical Garden and the University of Puerto Rico (H. Madden, pers. comm.).

Boldingh (1909) considered the vegetation of the three Windward Islands (St. Eustatius, Saba and St. Maarten) in general to be identical to each other with a particular formation being predominant on each island. Boldingh (1909) distinguished four vegetation types on St. Eustatius:

- 1. Vegetation of the higher parts of the mountains ('Eriodendron vegetation').
- 2. Vegetation of the Cultuurvlakte and the lower parts of The Mountains ('Croton vegetation').
- 3. Vegetation of the seashore and the rocky localities of the island ('Littoral vegetation').
- 4. Vegetation of the cultivated region ('Eriodendron and Croton vegetation').

The *Croton* vegetation was described as a dry, shrubby vegetation of a grayish aspect that dominated in the Cultuurvlakte but was also found on the hills near Signal hill and Concordia. The *Eriodendron* vegetation was pictured as a greenish woody vegetation that covered the higher parts of The Mountains and the Quill. The invasive *Antigonon leptopus* is only mentioned by Boldingh (1909) as cultivated in a garden of the capital of St. Eustatius.

The vegetation study of Stoffers (1956) of St. Eustatius and the other two Windward Islands (Saba and St. Maarten) resulted in the description of 28 different vegetation types that were classified in three groups: primary climatic climax communities, primary edaphic climax communities and secondary and sub-climax communities. This classification system is based on previous work by Beard (1944, 1949 and 1955) (see also Howard 1973). For St. Eustatius Stoffers (1956) distinguished 18 different vegetation types from the three groups mentioned (but mapped only 15). According to Stoffers (1956) the vegetation types were mainly determined by climatic factors.

The present study and the publications on the flora of St. Eustatius (Arnoldo 1971; Stoffers 1963-1984, 1981; Howard 1974-1989; Rojer 1997) have served to determine that the) flora of the island consists of some 505 species in 345 genera and 94 families; 15 % of the plant species does not occur on St. Maarten (34 km²) or Saba (12 km²). In connection with this it can be mentioned that the flora of Saba and St. Maarten consist respectively of 565 and 544 species. All three islands have a relatively higher plant biodiversity per unit surface area compared to the southern Caribbean island of Curaçao: the flora of Curaçao consists of 492 plant species and the surface of Curacao is 444 km² (Beers *et al.* 1997). Curaçao has a semi-arid climate and has the richest flora of the Leeward Dutch Antilles. Further research is underway by the New York Botanical Garden and the University of Puerto Rico. More recent research on orchids has revealed new species for the island (H. Madden, pers. comm.).

The main families of the flora of St. Eustatius are:

Gramineae (39 spp., 25 genera), Polypodiaceae (30 spp., 15 genera), Fabaceae (26 spp., 17 genera), Compositae (24 spp., 21 genera), Rubiaceae (23 spp.18 genera). These same families (although the last three in a slightly different sequence of importance) are the most important ones on the sister island of Saba: Gramineae (51 spp.), Polypodiaceae (43 spp.), Compositae (34 spp.), Rubiaceae (23 spp.) and Fabaceae (22 spp.). For sister island St. Maarten the sequence is as follows: Gramineae (65 spp.), Compositae (31 spp.), Euphorbiaceae (30 spp.), Fabaceae (28 spp.) and Malvaceae (21 spp.).

The following data show the grade of (dis)similarity among the flora of the three Windward Islands of the Dutch Antilles. The combined known flora of the three Windward Islands consists of 857 species.

Table 1 Similarity of the flora of the three Dutch Windward islands of St. Eustatius, Saba and St. Maarten

	% of total of 857 spp. shared.							
All three islands	32 %							
St. Eustatius and Saba	10 %							
St. Eustatius and St. Maarten	9 %							
Saba and St. Maarten	7 %							
Part of the 857 spp. found only on a single island	42 %							

Most species of St. Eustatius have a wide distribution on the American continent (52 %), followed by the species with a world-wide distribution (29 %). Next are the West-Indian species (15 %), the species restricted to the Lesser Antilles (4 %) and finally the St. Eustatius island endemics (< 1 %). The latter group consists of only one species: *Ipomoea sphenophylla* Urban (Howard 1989b; Howard & McDonald 1995). Some species of the group that is restricted to the Lesser Antilles have a very small geographic distribution area: *Agave vangrolae* Trel. occurs only on St. Eustatius, St.Kitts and Nevis (Howard 1979), *Chromolaena* (= *Eupatorium*) *macranthum* Sw. on the same islands and on Saba (Howard 1989a), *Begonia retusa* O. Schulz on St. Eustatius, St. Kitts, Saba, St.Barts and Montserrat (Howard, 1989b), *Myrcia citrifolia* (Aublet) Urban *var. imrayana* (Griseb.) Stehlé & Quantin on the Lesser Antilles and Puerto Rico (Howard 1989b). *Aristida suringari* Henr. has a limited distribution in the Lesser Antilles, but occurs also on Aruba and Bonaire (Stoffers 1981). Based on their limited geographic distribution and the fact that they are endemic to a small range of islands, these species should also be considered as "endemics" and receive adequate protection.

2.4.2 Human influence on flora and vegetation

It may be assumed that before the colonization of St. Eustatius by the Europeans human influence on flora and vegetation was relatively limited. While the pre-colonial Amerindian inhabitants did use heavy timbers for canoes and posts for their huts and also practiced limited cultivation of several crop species (Versteeg & Schinkel 1992), their impact cannot be compared to that by industrial man after colonization. The pre-colonial native inhabitants of the Caribbean widely transported animals and plants of value as food (Berman & Pearsall 2000; Hofman & Hoogland 2003) and probably also introduced tree species of food value, such as possibly Annona muricata, A. squamosa, Opuntia spp., Melicoccus bijugatus, and Morisonia americana. In 1636 the island was occupied by Dutch colonists (De Palm 1985). Until 1784 the island played an important role as a center of trade and as slave depot (2000- 3000 slaves/ year). Trade brought such a great wealth to the island, especially during the second half of the 18th century when the merchants profited from the American wars of liberation, that the island was known as The Golden Rock. An average of 3000 ships per year anchored at its coast then. As a trade island, plantations were of less importance but there was cultivation of sugar cane, indigo, cotton and food crops. At the end of the 18th century the number of (very small) plantations was 76 (1775) and their main product was sugar cane. Cattle breeding was then a secondary activity (De Palm 1985). In the 20th century attempts were made with the cultivation of sisal, but this was not successful.

During the first half of the 19th century cultivation of sugar cane was still the main economic activity for the island. Teenstra (1977) makes mention of the panoramic view from The Quill onto the mass of sugar cane fields in the middle of the island, as well as in the area of The Mountains. The fact that the island lacked woods that could be used for the construction of sugar barrels and firewood (Teenstra 1977) is an indication that extensive woodcutting had taken place in those days. Teenstra (1977) also mentions the influence on the native vegetation of plant species that were imported for horticulture and occurred e.g. in the crater of The Quill (banana, soursop and coffee). At the beginning of the 20th century there were still some plantations in the level parts of St. Eustatius (Boldingh 1909). In 1950 a considerable part of the Cultuurvlakte was still under cultivation for the production of subsistence crops and cattle ranching

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(Veenenbos 1955). On the small plateau of Little Mountains and Mary's Glory, agricultural activity took place, while in the remaining part of The Mountains semi-feral goats were grazing. The glacis east and west of the Quill which was formerly under cultivation, producing mainly sugarcane and cotton, were largely covered with brush at that time. In 1952 and 1953 the negative influence of cattle and goats on the native vegetation was clearly visible, felling of trees took place on the slopes and rim of the Quill and charcoal burning was a frequent activity in The Mountains (Stoffers 1956).

At the time of the fieldwork for the present study, only a small part of the Cultuurvlakte was still under cultivation. A larger part of this area and parts of the lower slopes of The Quill were still in use for cattle grazing. Free roaming goats were active everywhere else including the crater and the area of the rim of the Quill. Furthermore, at the time of the fieldwork for the present publication the oil terminal, which has been present in the western part of The Mountains since 1982 (De Palm 1985) covered only approximately 0.5 km². The area in use has since become larger.

During the 18th century the population of St. Eustatius reached its historic maximum and consisted of over 25.000 people (Teenstra 1977). After the decline of trade, many people left and in 1827 only 2273 people still lived on the island. This number continued to decline to 1325 in 1910 and 970 in 1950. This was after many men had left the island to work at the refineries in Aruba and Curaçao. After the establishment of the oil terminal on St. Eustatius the population increased again to about 1900 people in 1996 (CBS 1996).

3 Methods

3.1 Photo-interpretation and fieldwork

For the survey of the (semi)-natural vegetation of St. Eustatius, the landscape guided method, developed at the International Institute for Aerospace Survey and Earth Sciences (ITC) was applied. The principle of this method is a combination of aerial photo-interpretation (API) and stratified sampling (Zonneveld 1979, 1988a, 1988b; Van Gils *et al.* 1985; Groten *et al.* 1991). Stereoscopic photo-interpretation was based on true colour aerial photographs of the island (scale approximately 1:8,000) that were taken in March and April 1991 and formed the basis for field sampling. The photo-interpretation was based on analysis of differences in photo-features, such as tone, texture and spatial pattern, using the landscape as guiding principle. The resulting units of the photo interpretation were drawn on a 1:10,000 topographic map (1982; Dienst Kadaster van de Nederlandse Antillen). This map (base map) was used for field-truthing and determination of the location of the sample plots. Sample plots were selected in each mapping unit of the base map (stratified sampling). At each site the plot was haphazardly selected in a representative area of the unit. A varying number of sample plots ('relevé's') were taken in each of the (preliminary) mapping units. Plot sizes used, were based on the guidelines of the ITC method, but in the present study slightly modified for herbaceous vegetation types (a), woodlands (d) and heterogeneous higher vegetation (e) (Van Gils *et al.* 1985):

Short grass and herb vegetation: 3m x 3m
 Low shrub vegetation (<1 m): 5m x 5m
 High shrub vegetation (> 1 m): 7m x 7m
 Woodland: 10m x 10m
 Very open heterogeneous higher vegetation: 15m x 15m

On St. Eustatius a total of 84 plots were sampled for use in data analysis. The sample locations were marked and given a number on the aerial photographs and on the base map, to facilitate future reference.

3.2 Data collection

The fieldwork on St. Eustatius was done in September and October 1999. All data collected for each sample plot were recorded on standard ITC relevé sheets (see e.g. Loth 1990). These data included:

Terrain characteristics: information on geology; relief type; slope type (steepness and exposure); percentage of surface stoniness or rock outcrops.

Soil and water characteristics: pH of the top layer (using Hellige indicator solution) and relative calcium-carbonate content (using HCl); soil colours were assessed with Munsell colour charts; coverage of the soil / rocks with plant litter as percentage of the sample plot.

Grazer presence: In order to have an assessment of the impact of disturbance on the vegetation the presence of fresh or relatively recent goat excrements in the sample plot was recorded. In cases where the goat dung was only found outside the plot, this was noted separately on the sheet.

Vegetation structure and floristic composition: total real cover; cover and height (average and maximum) of each stratum. When it was difficult to distinguish between a shrub layer and a tree layer or a shrub and a herb layer, these were considered as one layer. Sometimes the tree and/or shrub layer could be divided into a higher and a lower layer. In each plot all species were recorded for each stratum

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and their abundance or coverage were estimated. Coverage estimates were transformed to the decimal scale for recording coverage in vegetation analysis according to Londo (1976).

The following publications were used for the identification of the plant species of St. Eustatius: Boldingh (1913), Hitchcock (1936), Arnoldo (1954), Stoffers (1963-1984), Little & Wadsworth (1964), Pinto-Escobar & Mora-Osejo (1966), Little et al. (1974), Godfrey & Wooten (1979) and Howard (1974, 1977, 1979, 1988, 1989a & b), Correl & Correll (1982), Liogier (1985-1997). While Axelrod (2011) provides updated names for many of the species treated (Appendix 4), because of their wider availability, nomenclature of the plant species is based on Howard (1974, 1977, 1979, 1988, 1989a & b), except for species not treated by Howard, in which case we used Stoffers (1981). Names for fern species are based on Proctor (1989). Some plant species proved difficult to identify; when only the genus could be determined, the genus name is followed by the extension 'spec.'

3.3 Data processing

A total of 335 plant species was recorded in the 84 sample plots used. Table 2 shows the conversion of the 14 categories of the Londo (1976) scale to a scale of 9 scores for input into the clustering program TWINSPAN (Two-Way Indicator Species Analysis; Hill 1979) which served to distinguish the vegetation types. Field observations helped to identify misplaced samples and these were moved to the most appropriate vegetation type. After accomplishing the final vegetation table via TWINSPAN, a synoptic table was made with the program CLUTAB (Wageningen Agricultural University 1994) to help further characterize the vegetation types (Appendix 1). In the synoptic table, the presence or absence in a cluster is indicated for each of the 335 plant species and a frequency scale of I-V is used as an index of species presence. A distinction was further made between differentiating species, common species, other species (occurring in maximally three clusters or in maximally five clusters but then with low presence) and rare species (Beers & Van Der Have 1989; Bokkestijn & Slijkhuis 1987; Bolman & Nijhof 1993).

Table 2 Decimal scale for abundance / coverage after Londo (1976) and the conversion values applied for the TWINSPAN clustering program

Londo ^a	r	р	а	m	1	2	3	4	5	6	7	8	9	10
Twinspan	1	2	3	3	4	5	6	7	7	8	8	9	9	9

Legend

 a r = rare, sporadic, p = rather sparse, a = plentiful, m = very numerous; overall cover < 5%; cover: 1 = 5-15%; 2 = 16-25%, etc.; 9 = 96-100%.

3.4 Final map compilation

After classification of all sample points into the present vegetation types, each sample point was labelled with a code corresponding to the specific vegetation type to which it belongs. By plotting these codes onto the aerial photographs, the photo features could be compared for each plant community and used to classify the interlying unsampled areas.

The hierarchical order used for the names of the land types in the final legend is as follows: (1) geology and land type; (2) terrain form (mountains, hills, lowlands, cliffs, beaches); and (3) vegetation structure and floristic composition (vegetation types). After preparation of the final legend, the aerial photographs were re-interpreted where necessary for the preparation of the final map. The re-interpretation was scanned and edited in ArcGIS into which also all information on topography, geology, landscape, soil characteristics and vegetation types were stored. The final map was made by combining within the

ArcGIS, the main topographic features and the vegetation communities. Because of practical reasons the scale of the final map was not set at 1:16,000, as would be the case considering the ideal 1:2 ratio of aerial photographs and final map (Van Gils *et al.* 1985; Loth 1990), but at 1:37,500 in order for it to be a semi-detail scale and to best compare the map with that of Stoffers (1956).

4 Results

4.1 Vegetation types

Cluster analysis of the 84 sample plots resulted in a total of 13 vegetation types. Each vegetation type is characterized by the presence or absence of (a combination of) certain species. The first part of the binary name represents a common and often dominant species with a high coverage. The second part of the binary name is a differentiating or accompanying species, occurring in at least 41% of the sample points of that type. When no differentiating species were present, the second-most important species for that type was taken to define the type. In two cases (Types 10 and 13) there was an exclusive dominant species and in this case only the name of this species was used to denominate the type. The synoptic table of the 13 vegetation types (Appendix I) gives the frequency of occurrence for each species per vegetation type.

The 13 vegetation types are described below. The sequence in which the vegetation types are described below does not follow their sequence in the synoptic table, but is in accordance with their dominance in the mapped landscape units, going from the highest areas to the lowest areas in both the Quill volcano area and the north-western volcanic hills (The Mountains) (see Tables 3 and 4).

At the end of the description of each vegetation type, values are given for the pH, slope and exposure, average number of species for each vegetation type, cover and average height of the vegetation (for calculating the average height of the vegetation type, the height of the most characteristic layer was averaged over all the sample plots). Each value for a parameter represents the average of all sample plots of a type, followed by the observed range between brackets. Table 3 shows the 13 vegetation types of the present study and their correlation with the soil- and land types of Veenenbos (1955).

4.1.1 Myrcia splendens - Quararibea turbinata type (2 relevés)

This vegetation type is characterized by the presence of big trees and a high total vegetation cover. The vegetation in the lower layers is sparse. The presence of big trees is the result of the humid climate that exists within the crater of the Quill and the fact that the vegetation is protected from the strong trade wind. The species composition is variable as a consequence of the fact that formerly grown commercial crops in the area nowadays form part of the naturalized vegetation. The number of species is relatively low in comparison to other vegetation types in the present study in which there is also a prominent tree layer. On the other hand this vegetation type is also characterized by a high number of plant species that occur exclusively in this type. The following differentiating species belong to this group of plants: Quararibea turbinata (a tree), Piper medium (a herb), Asplenium cristatum (a fern) Theobroma cacao (a formerly cultivaterd tree species), Hirtella triandra (a tree) and Faramea occidentalis (a tree). P. medium, Asplenium cristatum, Quararibea turbinata, Ocotea spec., Psychotria spec., Theobroma cacao, Hirtella triandra, Philodendron lingulatum, Coccoloba venosa, Faramea occidentalis, Ficus trigonata, Picrasma excelsa and Polypodium phyllitidis are exclusive species (Arnolds 1983) for this type. Q. turbinata (V(4)), P. medium (V(3)), Psychotria spec. (V(3)), Ocotea spec. (V(3)) are also constant species (Arnolds 1983). Furthermore three species that on St. Eustatius occur in only a few natural vegetation types are common in this type: Myrcia splendens, (shrub or tree) Casearia decandra (shrub or tree) and Allophyllus racemosus (shrub or tree). Fern diversity is high and many climbers and lianas are found in the trees: e.g. Smilax guianensis, Pisonia aculeata and Hyperbaena domingensis. Epiphytic as well as terrestrial Araceae are present, the latter in the open herb layer in which the grass Pharus glaber dominates.

The ground surface of the crater consists of big boulders covered with mosses between which soil is present. This soil is very shallow coarse sandy loam described as 'Stony rough land'. A significant layer of plant litter covers up to 80 % of the surface. The vegetation is considered a primary climatic climax plant community and comparable to the evergreen seasonal forest of Stoffers (1956) (see Table 5).

pH 7.5

Slope 12° (10-13°) Exposure e / nnw

HCI -

of species 27 (23-29)

Total real cover 82 % (79-85 %)

Height of trees/shrubs 10.3 m (2.5-18.0 m)

4.1.2 Coccoloba swartzii - Ardisia obovata type (3 relevés)

This type is characteristic for the rim and the highest parts of the steep slopes of the Quill and has the highest average species diversity of all 13 vegetation types of St. Eustatius. Evergreen trees and shrubs determine the appearance of the vegetation. An open high tree layer usually overtops a high shrub/low tree layer. This top layer is absent on the top of the rim. Coccoloba swartzii, Guettarda scabra, Myrcia citrifolia and the differentiating species Ardisia obovata (a tree) have a high cover. The trees Clusia major (epiphytic) and Byrsonima spicata are other important differentiating species. Myrcia citrifolia is found in only one other vegetation type (type 3). The following exclusive species (Arnolds 1983) for this type can also be identified: A. obovata, B. spicata, C. major, Eupatorium macranthum, Melothria pendulum, S. lancifolium, Pimenta racemosa, Ficus citrifolia, Miconia laevigata, Epidendrum ciliare and Spondias mombin. The first three species are also constant species (Arnolds 1983). Spondias mombin is one of the two deciduous species in the tree layer. The absence in this type of the otherwise quite common tree species Pisonia subcordata is noteworthy. The evergreen Eugenia ligustrina (shrub or small tree) is abundant in the shrub layer. Ferns, Araceae, epiphytic bromeliads and the orchid Epidendrum ciliare are often present. The open herb layer consists mainly of the grass Panicum trichoides and the herb Peperomia myrtifolia. Mosses and lichens can be found on trees and stones. This vegetation type harbors moss species with a more restricted geographical distribution (Wiersma 1984). Broken branches and fallen trees are a common feature of this vegetation type and are the signs of damage by past hurricanes.

The soil is a very shallow coarse sandy loam of the 'Stony rough land' type. The vegetation is considered a primary climatic climax plant community and is comparable to the dry evergreen forest of Stoffers (1956) (see Table 5).

pH 6.0 HCI -

 Slope
 41° (36-46°)

 Exposure
 ssw / wsw

 # of species
 46 (31-55)

 Total real cover
 64 % (60-70 %)

 Height of trees/shrubs
 3.3 m (2.5-4.0 m)

4.1.3 Chionanthus compacta - Nectandra coriacea type (9 relevés)

This vegetation type has no differentiating species. It occurs all around the Quill just below vegetation type 2, where slopes on average become less steep. The altitudinal lower limit for this type is about 200 m. This type also has a relatively high average number of species, but contains a somewhat smaller

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number of species compared to type 2. There is a combined tree and shrub layer which on the northwestern slope is overtopped by a higher tree layer up to 14 m high on average, consisting of e.g. Ceiba pentandra and Spondias mombin. Different tree species that are generally uncommon, reach their highest abundance in this vegetation type: Chionanthus compacta, Casearia decandra, Citharexylum spinosum, Erythroxylum havanense, and Maytenus laevigata. Climbers occur very frequently (Cissus sicyoides, Macfadyena unquis-cati and Capparis flexuosa). Ferns and epiphytic Bromeliaceae sometimes occur less frequently and have a low cover while Aracaea are very scarce. The herb layer is very open. This type and type 2 have several species in common that occur practically only in these two types (Ardisia obovata, Chionanthus compacta, Ficus citrifolia, Inga laurina, Miconia laevigata, Myrcia citrifolia, Ocotea patens, Pimenta racemosa, Spondias mombin, and Zanthoxylum martinicensis). Also several species are found whichoccur in only one other vegetation type but in which they have a much lower frequency of occurrence (Allophyllus racemosus, Anthurium grandifolium, Bernardia corensis, Byrsonima spicata, Casearia decandra, Catopsis floribunda, Chiococca parvifolia, Chionanthus compactus, Elaphoglossum rigidum, Eugenia axillaris, Guettarda scabra, Maytenus laevigata, Myrcia splendens, Nectandra coriacea, Panicum trichoides, Pharus glaber, Polypodium pectinatum, Psychotria nervosa and Smilax guianensis).

Most of the soil surface in this type is covered with big stones on which mosses and lichens flourish. Litter is abundant (average of 41 % cover of the sample plot) while tree damage caused by past hurricanes is noticeable in this type. The soil is mostly of the 'Stony rough land' type which is very shallow and stony and consists in this case of coarse sandy loam. 'Statia sandy loam, steep phase' (very stony) is also present and is the best soil of St. Eustatius. Its internal drainage is good and the organic content increases with height. Its parent material has a great porosity, though in the steep phase, moisture retention conditions are rather well (Veenenbos 1955).

The vegetation is considered a primary climatic climax plant community and comparable to the semievergreen seasonal forest of Stoffers (1956) (see Table 5).

pH 7.1 HCI -

 Slope
 34° (27-45°)

 Exposure
 wsw / nnw / e

 # of species
 38 (26-50)

 Total real cover
 60 % (40-75 %)

 Height of trees/shrubs
 4.6 m (2.5-6.0 m)

4.1.4 Pisonia subcordata - Eugenia axillaris type (7 relevés)

This vegetation type is intermediate between type 3 and 5 in terms of average number of species, total real cover and height of the combined tree and shrub layer. The average slope value is lower compared to the value for type 3 or 5 and therefore represent relatively drier circumstances. No differentiating species were identified. *Pisonia subcordata* is very abundant in the mostly combined tree/shrub layer and reaches its highest frequency and cover in this vegetation type. Other species that reach their highest frequency and often their highest cover in this type are *Eugenia axillaris*, *Randia aculeata*, *Bourreria succulenta* and *Capparis indica*. *Erythroxylum havanense* and *Guettarda scabra* are other frequent tree species in this type. The shrub *Rauvolfia viridis* and the liana *Stigmatophyllon periplocifolium* occur very frequently. The epiphyte *Tillandsia utriculata* occurs regularly and ferns are absent. Mosses and lichens are scarce and the herb layer is very open.

Vegetation type 4 is mainly found on the lower south-western slopes of the Quill, areas that were formerly used as farmland, but which have since been recovering from deforestation. It also occurs on a part of the slope above White Wall.

Two soil types are present in this vegetation type: 'Stony rough land' and 'Statia sandy loam' (mostly). The latter one is represented by the steep and moderately steep phases.

pH 7.2

HCI
Slope 23° (10-32°)

Exposure e / s / nw

of species 31 (22-42)

Total real cover 53 % (42-72 %)

Height of trees/shrubs 3.4 m (2.8-4.5 m)

4.1.5 Pisonia subcordata - Justicia sessilis type (11 relevés)

This type is found only in the more wooded parts of the northern hills of 'The Mountains'. The salient structural feature is the tree/high shrub layer that is relatively quite high and rich in species. The highest trees occur in the valleys and on the steep upper parts of the leeward slopes. *Morisonia americana* (a tree; *Capparaceae*) and *Piscidia carthagenensis* (a tree; *Fabaceae*) are differentiating. *Pisonia subcordata, Morisonia americana, Samyda dodecandra* and *Eugenia ligustrina* occur very frequently and reach some of their highest cover value in this type. Despite the high frequency of *Pisonia fragrans, Piscidia carthagenensis* and *Bursera simaruba* they do not dominate the aspect of the vegetation. About half of the trees and high shrubs are deciduous whereas the other half is evergreen. A small number of species are thorny: *Randia aculeata, Comocladia dodanaea* and two cactus species (*Opuntia triacantha* and *Pilosocereus royeni*). *Pilocereus royeni* has its highest frequency and cover in this vegetation type. The epiphytic *Tillandsia utriculata* can be seen regularly. Two climbers are common: *Heteropteris pupurea* and *Stigmaphyllon emarginatum*. The open herb layer consists mainly of *Commelina elegans* together with the differentiating species *Justicia sessilis* and *Setaria rariflora*. About 30 % of the surface is usually covered with stones on which mosses and lichens may be present.

The soil is predominantly of the 'Stony rough land' type. In this case, very shallow gritty stony clay loam overlies the hard bedrock. "Terras Loam' and 'Zeelandia loam' (alluvial fan phase) occur occasionally. The 'Terras Loam' soil does not have a pronounced soil formation, is poor in nutrients, has a low internal drainage and shows severe sheet erosion. In areas with slopes over 20% as a rule nearly the entire original soil surface is gone.

pH 7.1 HCl -

 slope
 37° (27-49°)

 exposure
 ese / wsw / n

 # of species
 33 (21-44)

 total real cover
 47 % (33-53 %)

 height of trees/shrubs
 3.6 m (1.5-5.0 m)

4.1.6 Capparis cynophallophora - Gymnanthes lucida type (4 relevés)

This vegetation type has some characteristics in common with vegetation type 5: their average slope value and total real cover are very similar. They further have in common a number of the same species that play an important role in both vegetation types (*Bursera simaruba*, *Bourreria succulenta*,

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Erythroxylum havanense, Samyda dodecandra, Randia aculeata, Heteropteris purpurea, Pisonia subcordata, Capparis cynophallophora, Comocladia dodonaea, Tillandsia utriculata, Setaria rariflora, Solanum racemosum and Cephalocereus royení). Vegetation type 6, however, has a considerably lower species diversity and lacks some very prominent/characteristic species of type 5 (Justicia sessilis, Pisonia fragrans, Stigmatophyllon periplocifolium, Rauvolfia viridis, Eugenia ligustrina and Morisonia americana). Trees are relatively high (the max. height of trees measured in the plots is 6.4-8.0 m). The tree Capparis cynophallophora is dominant in the present vegetation type while Pisonia subcordata is also present in all sample plots. The only differentiating species is the tree Gymnanthes lucida that also is an exclusive species for this type (Arnolds 1983). Tillandsia utriculata (epiphyte), Erythroxylum havanense and Krugiodendron ferreum, are important accompanying species in the combined tree/shrub layer. Both deciduous and evergreen species are present in this layer. Mosses are always present, lichens only occasionally. Vegetation type 6 occurs on the lower slopes at the eastern side of the Quill and in the guts west of White Wall. The ground surface is covered with soil, which in the "guts" (ravines) gave a positive reaction with HCI, but on the lower slopes of the Quill was acidic. Loose stones are present on 25 % of the ground surface. The soil is completely of the 'Stony rough land' type and consists of very shallow coarse sandy loam.

pH 6.9
HCl +/slope 35° (10-46°)
exposure e / ssw
of species 19 (17-19)
total real cover 51 % (42-63 %)
height of trees/shrubs 4.6 m (3.5-6.0 m)

4.1.7 Antirhea acutata - Dodonaea elaegnoides type (6 relevés)

In general evergreen shrubs or small trees are the most frequent species found in this type and three of them (*Antirhea acutata*, *Dodonaea elaeagnoides*, *D. viscosa*) are also differentiating. The first species is the most common species of this type (IV(3) and all three species are exclusive (Arnolds 1983) for this type. This vegetation type is found in the southern part of St. Eustatius (White Wall and the steep rocky parts of the Big Gut area). It is a shrubby vegetation and has on average the lowest coverage of all types in the present study. The small evergreen tree *Crossopetalum rhacoma* occurs frequently. *Agave spec.* can be seen occasionally. A number of grasses and a few *Cyperaceae* occur, amongst which *Aristida adscensionis* and *Paspalum laxum* occur most frequently. Mosses occur sometimes.

The surface is partly rocky and also calcareous. The shallow and stony soil is completely of the 'Stony rough land' type.

pH 8.1

HCI +
slope 41° (20-57°)
exposure sse / ssw / wnw
of species 13 (5-18)
total real cover 27 % (3-35 %)
height of shrubs 1.5 m (0.3-2.5 m)

4.1.8 Pisonia subcordata - Ayenia insulaecola type (12 relevés)

This is a vegetation type that is found in disturbed areas: the surroundings of Billy's Gut, the lower Quill slopes, especially in the south near Toby Gut, and some open areas in The Mountains. It lacks a homogeneous structure: the tree layer is usually open or absent but sometimes rather closed. Where the tree layer is open or absent, the shrub and/or herb layer covers most. The composition of the tree layer is very variable and on average consists of a small number of species (5). Of the tree species only *Pisonia subcordata* has a high frequency. This is the second vegetation type in which the slender columnar cactus *Pilosocereus royeni* reaches its highest frequency, but in the present type its coverage is in the lowest cover class. The shrub and herb layers contain the most species. In the shrub layer the thorny species *Randia aculeata* and *Opuntia triacantha* are dominant. Other shrubs that occur frequently are: *Ayenia insulaecola* (differentiating species), *Jatropha gossypiifolia, Melochia tomentosa* and *Solanum racemosum. A. insulaecola* is an exclusive species (Arnolds 1983) for this type. Where the herb layer is well developed it consists mainly of the low shrub *Sidastrum multiflorum* and the invasive grass *Bothriochloa pertusa* (Indian couch grass). Mosses and lichens are very scarce.

The surface is usually covered by soil with hardly any stones. The soil type is mostly 'Stony roughland' (stony clay loam or coarse sandy loam, both very shallow and gritty) while 'Terrasloam' is of less importance.

pH 6.9
HCI Slope 22° (7-41°)
Exposure e / s / nw
of species 23 (13-33)

of species 23 (13-33)

Total real cover 43 % (26-60 %)

Height of trees/shrubs 2.6 m (0.2-5.8 m)

4.1.9 Rauvolfia viridis - Lantana involucrata type (5 relevés)

This is a low vegetation (because of the fact that the shrub and/or herb layer is the most important layer) with on average relatively high cover values. Sometimes scattered low trees (on average approx. 2 m high) are present. This is the vegetation type that has the second-highest number of differentiating species (six). These are: Lantana involucrata, Sida cordifolia, Sida glomerata, Boerhavia spec., Achyranthes asperac and Herissantia crispa. The latter species (a low shrub) is only found in this type (II(2)). The most common species in this vegetation type are Rauvolfia viridis and the thorny small tree Randia aculeata. Other frequently occurring species are the thorny Acacia macracantha and the low shrub Sidastrum multiflorum. The common invasive grass Bothriochloa pertusa has a large cover within this vegetation type. A salient feature is that despite the fact that it is a disturbed vegetation, no cacti occur. The litter percentage (10%) is low compared to the total real cover. This might be caused by the influence of the wind. Mosses and lichens are absent. This vegetation type is only found on the weak slopes of the lowest parts of the eastern and northern sides of the Quill. These areas were used or are still in use as pastures for exotic grazers (cattle, sheep, goats, donkeys). Dominance of thorny species is often the result of grazing by introduced mammals (Debrot & De Freitas 1993; National Park Service et al. 2008).

The soil is completely of the 'Statia sandy loam type, moderate steep phase'.

pH 7.2 HCl -

Slope 13° (4-27°)

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Exposure wnw / nne / sse # of species 20 (13-26)
Total real cover 53 % (28-75 %)
Height of shrubs/herbs 0.8 m (< 0.1-1.6 m)

4.1.10 Antigonon leptopus type (5 relevés)

This vegetation type is the second poorest in species of all vegetation types in the present study. The invasive vine *Antigonon leptopus* determines in most cases the appearance of this type because it determines its total cover. The herb layer is the most important layer. Some low shrubs are present and sometimes also scattered higher shrubs or trees. This vegetation type occurs in two different areas: in the surroundings of Billy's Gut together with types 8 and 11 and on the foot planes of the Quill along type 9. In the surroundings of Billy's Gut, trees or high shrubs can be seen e.g. one or more of the following species *Citharexylum spinosum*, *Piscidia carthagenensis* and *Annona squamosa*. Trees are absent from this type in the Quill area. *Antigonon leptopus* (IV(8)) and *Jatropha gossypiifolia* (IV (2)) are the only common species in this type. Differentiating for this type is an undetermined *Cyperus species* (*Cyperus spec.*). Among the few other species present, grasses are the best represented e.g. *Tragus berteronianus* and *Setaria setosa*.

The surface consists of soil. This soil is 'Statia sandy loam' moderate steep phase', 'Terras loam' or less abundant typical 'Statia sandy loam', which is the best soil of St. Eustatius.

pH 7.2

HCl Slope 4° (0-7°)

Exposure ese / w

of species 9 (4-22)

Total real cover 68 % (50-95 %)

Height of herbs 0.3 m (< 0.1-0.7 m)

4.1.11 Bothriochloa pertusa - Jatropha gossypiifolia type (5 relevés)

This vegetation type is a species-poor vegetation in which the invasive perennial grass species *Bothriochloa pertusa* is the dominant species and reaches its highest presence and cover (V(6)). No differentiating species were identified. Besides the structurally most important herb layer, usually an open low shrub layer can be distinguished in this type. Also the shrub *Jatropha gossypiifolia* reaches its highest presence and cover in this type (V(3)). The shrub *Solanum racemosum* occurs quite frequently (III(2)). The high presence of *Acacia* shrubs (III(2))indicates human disturbance (Debrot & De Freitas 1993, National Park Service *et al.* 2008). This vegetation type is found in the surroundings of Billy's Gut, on the cliff south of Oranjestad and also to a small extent in the northern hills. In all these locations grazing by goats and/or cows take place. The soil consists for the greater part of 'Statia sandy loam' and some 'Stony rough land' (shallow gritty stony clay loam).

pH 6.6 HCl -Slope 19°

 Slope
 19° (4-58°)

 Exposure
 e / sse / w / n

 # of species
 10 (5-23)

 Total real cover
 42 % (15-57 %)

 Height of herbs
 0.3 m (< 0.1-1.1 m)</td>

4.1.12 Bothriochloa pertusa - Bouteloua americana type (5 relevés)

Similar to vegetation type 11, the prominence of grasses is also characteristic for this type, although it is not realized by the dominance of only one species, but by a combination of several species (mainly *Bothriochloa pertusa*, *Tragus berteronianus* and *Bouteloua americana*). Type 12 is richer in species, but has a lower average cover in comparison to type 11. Just like in type 11, the invasive *B. pertusa* is also dominant in this type, but contrary to type 11, differentiating species were identified for type 12: *Desmodium triflorum* and *Bouteloua americana*. *Desmodium triflorum* has not been found in any other vegetation type on St. Eustatius outside type 12. In type 12 the shrub *Melochia tomentosa* reaches its highest frequency of the seven vegetation types in which it occurs (V(2)). The higher species diversity of type 12 in comparison to type 11 is reflected in the presence of the following species in type 12 but not in type 11: *Stigmaphyllon emarginatum* (woody vine), *Portulaca oleracea* (herb), *Tragus berteronianus* (grass), *Ruellia tuberosa* (herb) and *Pedilanthus tithymaloides* (shrub). *Coccoloba uvifera* (shrub/tree) and *Melocactus intortus* (cactus) occur occasionally. Vegetation type 12 is mainly found in The Mountains and to a smaller extent on cliffs.

The surface consists partly of rocks (8-60 %). The soil type is mostly 'Stony rough land' (with shallow gritty stony clay loam). 'Terras loam' occurs only rarely.

pH 6.8

HCl slope 31° (24-36°)

exposure nne / se

of species 15 (9-21)

total real cover 33 % (19-52 %)

height of herbs 0.3 m (< 0.1-0.8 m)

4.1.13 Coccoloba uvifera type (10 relevés)

This shrubby tree vegetation is on average the most species-poor vegetation of the island. The only common (dominant) species in this type is the shrub or tree *Coccoloba uvifera* (V(6)). This species is also differentiating and exclusive (Arnolds 1983) for this type. *Coccoloba uvifera*, appears either in the tree or in the shrub layer. All other low shrub and herb species occur in a (very) low frequency. Of these *Clerodendron aculeata* (climbing shrub) has the highest frequency (II(4)). This coastal vegetation can occur as beach vegetation as well as cliff vegetation. In the beach areas slope values of 0° -38° have been measured while on the cliffs, values up to 65° have been found.

Most of the time the surface consists of soil, but sometimes the surface is rocky. Where soil is present on steep cliffs, considerable wind and water erosion takes place. The soil at Concordia beach is alkaline (positive reaction to HCl), while the soil of the beach at Venus Bay is acidic (no reaction to HCl). The soil type is mostly 'Stony rough land' and less commonly 'Statia sandy loam'. The moderately steep phase of 'Statia sandy loam' and 'Zeelandia loam' of the alluvial fan phase occur even less.

pH 8.0

HCl +/slope 27° (0-65°)

exposure s / w / n / e

of species 4 (1-13)

total real cover 61 % (25-90 %)

height of shrubs 1.5 m (0.5-3.5 m)

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Table 3 Vegetation types versus the soil- and land types on and in which they are found. Soil- and land types are according to Veenenbos (1955).

SOIL- and LAND TYPE		Sm	Ss	TI	Za	Rs
VEGETATION TYPE						
1. <i>Myrcia - Quararibea</i> type						10*
2. Coccoloba - Ardisia type						10
3. Chionanthus - Nectandra type			2			8
4. Pisonia - Eugenia type		4	2			4
5. Pisonia - Justicia type				1 (Ts)	1	8
6. Capparis - Gymnanthes type						10
7. Antirhea - Dodonaea type						10
8. Pisonia - Ayenia type				3		7
9. Rauvolfia - Lantana type		10				
10. Antigonon type	2	4		4		
11. Bothriochloa - Jatropha type	8					2
12. Bothriochloa - Bouteloua type				2 (Ts)		8
13. Coccoloba type	3	2			1	4

^{*} Legend: (+ = cover < 5%); 1 = cover 5-14%, 2 = 15-24% etc., 10 = 95-100% Column: Rs = Stony rough land; SI = Statia sandy loam, base soil type; Sm = Statia sandy loam, moderately steep phase; Ss = Statia sandy loam, steep phase; TI = Terras loam; Ts = Terras loam, steep very stony phase; Za = Zeelandia loam, alluvial fan phase.

Table 4 Estimated cover of plant communities in the different (sub)landscape units. Based on plot data, filed observations and photo-interpretation

		Vegetation Type	Myrcia - Quararibea type	Coccoloba - Ardisia type	Chionanthus - Nectandra type	Pisonia - Eugenia type	Pisonia - Justicia type	Capparis - Gymnanthes type	Antirhea - Dodonaea type	Pisonia - Ayenia type	Rauvolfia - Lantana type o	Antigonon type	Bothriochloa - Jatropha type	Bothriochloa - Bouteloua type	Coccolobatype
Landscape Unit	symbol	#	10	2	3	4	5	6	1	8	9	10	11	12	13
Myrcia - Quararibea Mountains	M1	_	10											35	
Coccoloba - Chionanthus Mountains	M2	- 3	10	7	3		0		- 0	1	i i	1		(C.	2 4
Chionanthus - Nectandra Mountains, high variant		-		- 4	10		-	0 0	-			+ +		S.	1
Chionanthus - Nectandra M ountains, Ingil variant	M 3b	- 97			10		G.	6 1	. 3					G.	
Capparis - Pisonia Mountains	M4	- 8		2	10	2	3	5	- 0	3	82			3	0 - 0
	M5	- 0		100	1	10	3	3	9	3				3	3
Pisonia - Eugenia Mountains		- 33			8 3	10	8	-	-			8 8		35	: 5
Capparis - Antirhea Mountains	M6	- 3		4		-	9	5	5		4	-	_	27	
Pisonia - Antirhea Mountains	M7	- 4					-		2	8				-	
Antirhea - Coccoloba Mountains	M8	-						ļ	8						2
Rauvolfia - Antigonon Mountains	M9										7	3			
Pisonia - Justicia Hills	H1	- 3		× i		1	9				¥			8	
Pisonia - Bothriochloa Hills	H2	. 19					20			5			1	4	
Pisonia - Antigonon Lowlands	L1									5		- 5			
Bothriochloa - Antigonon Lowlands	L2									3-415-4		2	8		
Coccoloba Beach	В	92						10						No.	10
Coccoloba - Bothriochloa Cliffs	С	- 3		Š.			8		. 0				2	2	6

Legend: + = cover less than 5%, 1 = cover 5-14%, 2 = 15-24% etc. 10 = 95-100%.

4.2 Description of the final legend units

The main legend of the landscape ecological vegetation map of St. Eustatius is divided into five different landscape types (Fig. 5). The subdivision of these types is based on differences in vegetation. The names of the legend units refer to both terrain features and vegetation types. Table 4 gives a summary of the relative occurrence of the vegetation types in each of the listed (sub-) landscape types. The following landscapes and legend units have been distinguished:

M MOUNTAINS

The Mountains landscape is situated in the south-eastern part of St. Eustatius. It consists of a strato volcano, the Quill, rising up to 600 m. The Quill has a deep (330m between bottom and highest point of rim) and wide crater (750 m). Deep guts intersect its outer slopes. Two plates of sedimentary origin (White Wall and Sugar Loaf) interrupt the southern slope. The vegetation ranges from domination by big trees inside the crater to a low shrub and herb vegetation on the footplain outside the crater.

M1 MYRCIA -QUARARIBEA MOUNTAINS

This sub-landscape is restricted to the bottom and the lower inner walls of the crater. Its vegetation consists of the *Myrcia - Quararibea* type (Type 1) and is characterized by the presence of large trees (16-20 m trees in the upper layer).

M2 COCCOLOBA - CHIONANTHUS MOUNTAINS

This sub-landscape is characteristic for the highest parts of the rim and the highest slopes of the Quill. Except for a small area where this unit is not found, it occurs continuously around the volcano. The *Coccoloba - Ardisia* type (Type 2) is the main vegetation found, while the *Chionanthus - Nectandra* type (Type 3) is present but less abundant. Type 2 occurs higher on the slopes than Type 3.

M3a CHIONANTHUS - NECTANDRA MOUNTAINS, HIGH VARIANT

This higher variant of the *Chionanthus - Nectandra* Mountains is present on the shaded north-western slopes and in gullies on the northern and western slopes of the Quill. The vegetation consists only of the *Chionanthus - Nectandra* type (Type 3).

M3b CHIONANTHUS - NECTANDRA MOUNTAINS, LOW VARIANT

The lower variant of this sub-landscape surrounds the Quill just below the M2 landscape, however interrupted on the north-western slope by M5. The vegetation also consists of the *Chionanthus - Nectandra* type (Type 3), though on average the trees are 3.5 m lower than in M3a.

M4 CAPPARIS - PISONIA MOUNTAINS

This sub-landscape is mainly situated on the lower eastern slopes of the Quill and to a much lesser extent on the northern and north-western lower slopes. The generally rather heterogeneous tree vegetation (11 species on average) is a complex of the relatively more abundant *Capparis - Gymnanthes* type (Type 6) and the less abundant *Pisonia - Ayenia* (Type 8) and *Pisonia - Eugenia* (Type 4) types. Sometimes the vegetation is found on abandoned farmlands.

M5 PISONIA - EUGENIA MOUNTAINS

This sub-landscape is restricted to the lower western and south-western slopes of the Quill, as well as the slopes above White Wall. Relatively low trees and shrubs are characteristic for this unit in which only the *Pisonia - Eugenia* type (Type 4) is found. This vegetation is sometimes also found on abandoned farmlands.

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M6 CAPPARIS - ANTIRHEA MOUNTAINS

This sub-landscape occupies a relatively small area and is only found in the higher (steeper) part of the Big Gut area, on the southern side of the Quill. Two vegetation types are equally present: *Capparis - Gymnanthes* type (Type 6) and *Antirhea - Dodonaea* vegetation (Type 7). Type 6 is a relatively dense (avg. 50% cover) vegetation type that is characterized by the presence of relatively high trees (avg. 5.75 m and up to max. 8 m high) and Type 7 is a lower (avg. 1.5 m) and more open (avg. 26% cover) vegetation that's found on the rocky ridges.

M7 PISONIA - ANTIRHEA MOUNTAINS

This unit occurs on the south-western side of the Quill, on Docker's Island and near Toby Gut. Two vegetation types occur: *Pisonia - Ayenia* type (Type 8) and *Antirhea - Dodonaea* type (Type 7). Type 8 is by far the dominant vegetation type. The vegetation is characterized by a generally low and very open shrub layer (however, occasionally also very dense and higher) overtopped by a generally open (but sometimes also very dense) tree layer (4-6 m).

M8 ANTIRHEA - COCCOLOBA MOUNTAINS

This sub-landscape is only found in a small area in the southern part of St. Eustatius to the north of Back-Off Bay and is restricted to the steep rocky slopes of White Wall and Sugar Loaf, which both have calcareous properties ('White Wall formation'; Augustinus *et al.* 1985). The vegetation is predominantly of the *Antirhea - Dodonaea* type (Type 7), while the *Coccoloba uvifera* type (Type 13) occurs less frequent. A very open vegetation on the relatively steeper parts (47-54°) is alternated with a relatively more dense (35 %) variant on less steep parts (20-41°).

M9 RAUVOLFIA - ANTIGONON MOUNTAINS

This sub-landscape is mostly found along the coast on the lower eastern foot slopes of the Quill, while a small area is present to the north of the Quill near Mountain Piece. The vegetation is low (on avg. 0.9 m (range: 0.02-2.3 m) of shrubs, grasses and herbs and rarely a few scattered trees. It is predominantly of the *Rauvolfia - Lantana* type (Type 9) while the *Antigonon leptopus* type (Type 10) occurs sometimes. Parts of this landscape are in use as pastures.

H HILLS

The Hills landscape of St. Eustatius is found in the north-western part of the island ('The Mountains'). This landscape is characterized by a rough and irregular topography of steep hills (with 294 m as maximum height and slopes up to 49°) and deep valleys. Due to a fairly dry and sub-humid climate, soil formation is poor. A vegetation of rather low trees and shrubs covers most of this area, while an open grass/low shrub vegetation occurs on the more rocky parts.

H1 PISONIA - JUSTICIA HILLS

The *Pisonia - Justicia* Hills are found all over the Hills landscape especially in the valleys and on the leeward slopes of the hills. The tree/shrub or tree vegetation consists almost exclusively of the *Pisonia - Justicia* type (Type 5) while the *Pisonia - Eugenia* type (Type 4) is rarely found. The average height of the tree vegetation is approximately 2 m higher than when the highest layer of the vegetation is the combined shrub and tree layer (which on avg. is 2.9 m high).

H2 PISONIA - BOTHRIOCHLOA HILLS

This sub-landscape is mostly found on rocky soils and steep wind exposed slopes, including rather inaccessible areas. The main vegetation type is the *Pisonia - Ayenia* type (Type 8). Two other vegetation types also play a role of which the second one rarely occurs: *Bothriochloa - Bouteloua* type (Type 12) and *Bothriochloa - Jatropha* type (Type 11). Predominant features in the vegetation are low shrubs (< 1 m high) and grasses (one or two dominant species).

L LOWLANDS

The 'Lowlands' are the flatter area located between the Quill and The Mountains landscapes. It is called the 'Cultuurvlakte', which indicates its former use as farmland. This area is still used for cattle grazing and limited agriculture. The only area with more or less natural vegetation is found in the (north)western part, where Billy's Gut reaches the sea. The vegetation is a mosaic of a relatively open (but relatively high) tree layer and a low shrub vegetation that is often characterized by a high cover of one grass species.

L1 PISONIA - ANTIGONON LOWLANDS

This sub-landscape landscape occurs in the lower (almost flat) parts of the Billy's Gut area, often in gullies. Two vegetation types are equally important in this unit: *Pisonia - Ayenia* (Type 8) and *Antigonon* type (Type 10). Its structure is characterized by scattered groups of relatively high trees (avg. 5.75 m) in a low vegetation of shrubs in which vines reach high cover values and grasses occur abundantly.

L2 BOTHRIOCHLOA - ANTIGONON LOWLANDS

This sub-landscape is found in the higher parts of the Billy's Gut area, on the (almost flat parts of the) ridges between the gullies. Two vegetation types are found in this unit: the *Bothriochloa - Jatropha* type (Type 11) and to a much lesser extent the *Antigonon* type (Type 10). The low and generally relatively open shrub layer (when *Antigonon* is absent) is accompanied by a high cover of grasses (one grass species in general).

C CLIFFS

C1 COCCOLOBA - BOTHRIOCHLOA CLIFFS

The often steep cliff areas (>38°) are found all around St. Eustatius. The shrub vegetation is relatively (very) poor in species and can be open or more closed while the species composition is variable, although *Coccoloba uvifera* often is dominant. The *Coccoloba* type (Type 13) dominates the vegetation, while two other types occur occasionally (*Bothriochloa - Bouteloua* (Type 12) and *Bothriochloa - Jatropha* type (Type 11)). Parts of the Cliffs that consist of rubble and loose soil have a significant cover by grasses.

B BEACH

B1 COCCOLOBA BEACH

This *Coccoloba* Beach landscape occurs in two areas, e.g. along Venus Bay and along Concordia Bay. At Venus Bay the vegetation is a low shrub vegetation of approximately 1 m high on average and a cover above 50 %. This species-poor vegetation continues partly on the slopes of the hills. At Concordia Bay the landscape has a more dune-like character with a relatively higher vegetation (avg. 2.7 m and max. 5.2 m) and in which the combined tree and shrub layer is the highest layer. The *Coccoloba* type (Type 13) is the only vegetation type present.

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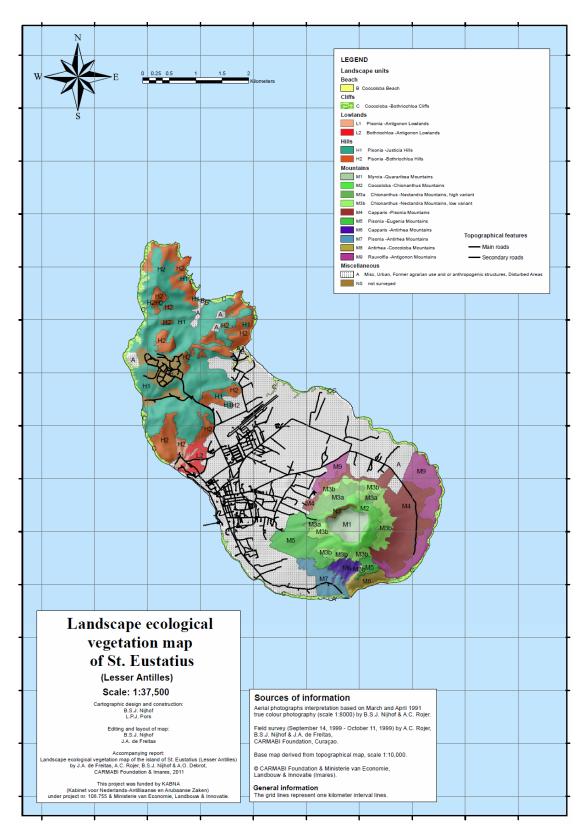


Figure 5. Vegetation map of St. Eustatius (digitally available from IMARES).

5 Discussion and conclusions

5.1 Anthropogenic effects

In the 18th century St. Eustatius was the most densely populated island of the three Windward Islands of the Dutch Antilles (Teenstra 1977). Based on the history of the island it must be concluded that through time most of the island's vegetation has experienced heavy and prolonged use by man for agricultural purposes and woodcutting. The effects of these activities are still noticeable today in various ways in different areas and vegetation types: through the absence of a tree layer, the dominance of species characteristic for disturbed vegetations, (relatively) low vegetation cover or the presence of exotic species. These are typical expressions of long-term anthropogenic impact (e.g. Debrot & De Freitas 1991, 1993, Weber 2005, Hardman 2009). Though at present agriculture and cattle breeding are of relatively little economic importance, livestock (mainly goats) still roam widely and graze in all the natural areas that were mapped in the present study. During our field work goats or their excrement were recorded in or in the direct vicinity of 68 % of the sample plots while other semi-feral livestock (sheep, cows, donkeys) or their excrement were seen in or in the direct vicinity of 19 % of the sample plots.

The type of dry forests present on St. Eustatius belongs to the most threatened ecosystems in Latin America (Ceballos & Garcia 1995). Helmer *et al.* (2008) used satellite imagery to study land cover and forest formation distributions for several adjacent islands, including St. Eustatius. They conclude that for several islands, land under cultivation has decreased over the second half of the 20th century by 60 to 100 percent while forest cover has increased. While fine resolution imagery was not available for St. Eustatius at that time, they concluded that while higher-elevation forests were generally well protected in reserves, rare drier lowland forests were poorly protected by the nature reserve systems, except for St. Eustatius where the two national parks protected 67% of the island's remaining driest forest.

A number of exotic (and known invasive) plant species were found in the vegetation types (*Antigonon leptopus, Bothriochloa pertusa, Catharanthus roseus, Leucaena leucocephala, Tecoma stans*) of which *Antigonon* is the worst because it entangles, overgrows and smothers other plant species (Stoffers 1984, Kairo *et al.* 2003, Weber 2005, Ernst & Ketner 2007, Langeland *et al.* 2008). One of the 13 vegetation types described in this study (Type 10) is dominated by this vine and is characteristic for disturbed sites near Billy's Gut, Schotsenhoek and the lower slopes of the Quill. This species is closely associated with the areas most intensively disturbed by man, most of which were not included in this assessment. Ernst & Ketner (2007) more recently mapped the distribution of *Antigonon* in St. Eustatius and found that it has expanded significantly, now occupying around 15-20% of the island. The (semi-natural) landscape types most affected by *Antigonon* today are M9 (e.g. seawards of the road to the Botanical Garden), M4 (e.g. inland from the road to the Botanical Garden), L2 (e.g. Godett Estate) and Cliffs (e.g. Smoke Alley). Without severe disturbance (roads, bulldozing, tilling, dumping of fill contaminated with seeds and tubers, erosion), the species has relatively limited potential to invade but once present, the ability of the species to persist and eventually dominate is great.

On the higher and lower slopes of the Quill a number of formerly cultivated exotic fruit tree species are common as part of the natural vegetation. From the higher slopes to the lower slopes these include: *Theobroma cacao, Melicoccus bijugatus, Annona muricata* and *Annona squamosa*. An undetermined (introduced) *Asparagus* species occurs also on the lower slopes of the Quill. The invasive grass species *Bothriochloa pertusa* did not occur on St. Eustatius in the 1950s (Stoffers 1956) but at present occurs in seven vegetation types on the island (Types 5, 7, 8, 10, 11, 12 and 13). It is more noteworthy and

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abundant in types 7 (*Antirhea-Dodonaea* type), 8 (*Pisonia-Ayenia* type), 11 (*Bothriochloa-Jatropha* type) and 12 (*Bothriochloa-Bouteloua* type).

Opuntia triacantha in The Mountains and Billy's Gut was much less abundant than expected based on Stoffers (1956). Despite the fact that this cactus was found in nearly all sample plots in these areas it did not occur there as a dense ground cover as found by Stoffers (1956). Opuntia dillenii present at the time of Stoffers was totally absent. It is very likely that this island-wide decline of Opuntia is caused by the arrival of Cactoblastis cactorum on St. Eustatius. This moth is known to destroy Opuntia plants (Habeck & Bennett 1998; Zimmerman et al. 2004; Zimmerman et al. 2005) and was recorded on the neighboring island of Saba (VAN HALTEREN 1994). Cactoblastis was introduced in 1957 in the Caribbean in Nevis to combat Opuntia curassavica and other Opuntia spp. and was very effective (Habeck & Bennett 1998; Zimmerman et al. 2005). From there the insect was brought in the years after to other Caribbean islands (Montserrat, Antigua and Gran Cayman). It had spread naturally to Puerto Rico and is now present in more Caribbean islands (St. Kitts, Guadeloupe, Haiti, Dominican Republic, the Bahamas) (Zimmerman et al. 2005).

The following plant species are protected in the St. Eustatius Flora and Fauna Ordinance, AB 1997, No. 06 and in the St. Eustatius Flora and Fauna Resolution, AB 1997, No. 07 (DCNA 2008): *Ipomoea sphenophylla* and the orchids: *Brassavola cucullata, Cyclopogon elatus* (formerly *Spiranthes elatus*), *Epidendrum anceps* (formerly *E. secundum*)), *Epidendrum ciliare, Epidendrum difforme, Jacquinella globosa, Liparis nervosa* (reports may be erroneous), *Mesadenus lucayanus, Microchilus hirtellus* (formerly *Erythrodes hirtella*), *Microchilus plantagineus* (formerly *Erythrodes plantaginea*), *Polystachya concreta, Psychilis correllii* (formerly *Epidendrum kraenzlinii*), *Tetramicra elegans* (may be same species as *T. canaliculata*), *Tolumnia urophylla* (formerly *Oncydium urophyllum*) (Stenapa 2008).

Ipomoea sphenophylla has been found in only vegetation type 5 and in the lowest frequency category with a low cover value (2). It occurs only in The Mountains and is a rare species (Howard 1989b; J. de Freitas, unpubl. data). Discovery of new sites for this rare species by Stenapa suggest recent expansion of the population of this island endemic (H. Madden, pers. comm). Of the 14 orchid species present on St. Eustatius, eight seem principally limited to the rim and crater of the Quill, while six are found in scattered numbers in areas of The Mountains. Of these six, three are presently known only from The Mountains, while two are widespread and more common on the island (B. cucullata and E. ciliare), and one appears to be widespread but rare (T. urophylla) (Stenapa 2008). Only T. urophylla is endemic to the Lesser Antilles (Howard 1974) and only Epidendrum ciliare was found in the sample plots for one or more of the vegetation types of the present study (types 2 and 4).

In addition, four areas are protected through this ordinance and accompanying resolution: the cliff wall in the Lower Town area along the length of the road from the harbor to the hairpin bend at Kings Well and three other areas: hilly areas of Boven, Venus, Gilboa Hill and Bergje (combined: 3.30 km^2); Signal Hill (0.44 km^2); and the exterior slope of the Quill from a height of 250 m, as well as the inside walls of the crater and the vegetation in the crater, and the section down to sea level known as White Wall (combined: 2.14 km^2).

5.2 Comparison of the vegetation types in the present study with those of Stoffers (1956)

Stoffers (1956) used the classification system of Beard (1944, 1949) for the tropical vegetation of the broader Caribbean region and divided the communities (i.e. the vegetation types) of the Windward Islands of the Netherlands Antilles into two main categories of climax communities, namely "Climatic" climax communities and "Edaphic" climax communities. On St. Eustatius he recognized 18 communities

of which he classified 10 as Primary climax communities (Montane thicket, Elfin woodland, Evergreen seasonal forest, Semi-evergreen seasonal forest, Deciduous seasonal forest, Dry evergreen forest, Evergreen bushland, Littoral woodland, Strand scrub community and *Hippomane* woodland). A comparison of the results of Stoffers (1956) with respect to vegetation types described in our study seems useful. The results of this comparison are presented in Table 5. The comparison reveals that only one vegetation type described in the present study corresponds closely with a community described by Stoffers (1956). This vegetation type is the *Coccoloba - Ardisia* type (Type 2) and it fits Stoffers' description of 'Dry evergreen forest' in species composition as well as in structure. Most of the other vegetation types described only partly correspond to the vegetations described by Stoffers (1956). This indicates that major changes have taken place in the intervening five decades.

Table 5 Correspondence between the vegetation types described in the present study and those of Stoffers (1956).

Stoffers (1956)	PRESENT STUDY
CLIMATIC COMMUNITIES	
Optimal formation	
Pioneer forest (VI*)	
Montane formations	
Montane ticket (VII)	related to Type 2 (Coccoloba - Ardisia type)
Elfin woodland (IX)	
Seasonal formations	
Evergreen seasonal forest (X)	Myrcia - Quararibea type (Type 1)
Semi-evergreen seasonal forest (XI)	Chionanthus - Nectandra type (Type 3)
Deciduous seasonal forest (XII)	Pisonia – Eugenia type (Type 4); Pisonia -
	Justicia type (Type 5)
Thorny woodland (XIII)	Rauvolfia - Lantana type (Type 9)
Leucaena thicket (XIV)	
Croton tickets (XV)	related to <i>Antigonon</i> type (Type 10)
Dry evergreen formations	
Dry evergreen forest (XVI)	Coccoloba - Ardisia type (Type 2)
Evergreen bushland (XVIII)	Antirhea - Dodonaea type (Type 7)
Thorny woodland (XIX)	
Croton tickets (XX)	Bothriochloa - Bouteloua type (Type 12)
Littoral woodland (XXI)	Coccoloba type (Type 13)
Vegetation of the rock pavement (XXII)	related to Type 7
Vegetation of rocky slopes (XXIII)	related to Types 12 and 13
EDAPHIC COMMUNITIES	
Strand scrub community (XXVI)	
Hippomane woodland (XXVIII)	

^{*}These Roman numerals correspond to those used by Stoffers (1956).

A comparison of Stoffers' Evergreen seasonal forest with our type 1 shows that our type lacks the following characteristic species of the Evergreen seasonal forest indicated by Stoffers (1956): Lonchocarpus violaceus, Andira inermis and Myrcia citrifolia. Hymenaea courbaril, described as a dominant species in the semi-evergreen seasonal forest in Stoffers (1956) was not found in our Type 3.

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Recent observations by Stenapa indicate *Bunchosia polystachia* has become an important component of the shrub layer in this vegetation type (H. Madden, pers. comm.) whereas it was not noted in 1999 or previously by Stoffers (1956). This may represent a recent development for this vegetation type, limited to the Quill crater. Beard (1949) considered *Bunchosia* as a typical species of semi-evergreen seasonal forest on several surrounding islands.

Both Types 4 and 5 resemble the deciduous seasonal forest of Stoffers (1956) with a high presence and cover by *Bursera simaruba* and *Pisonia* spp, although both lack a significant presence of a bromeliad in the herb layer and lack the upper layer of trees above 10 m described by Stoffers. Bromeliads in the herbaceous layer are extremely sensitive to ruminant grazers (Debrot & De Freitas 1993), and their apparent disappearance and degradation of this vegetation is probably due to the lasting high grazer densities in St. Eustatius. According to Stenapa the livestock at present amounts to approximately 1500 head of cattle, 2000 goats, 1000 sheep, 150 donkeys and 200 swine, of which 10-15% are kept fenced in (Jongman *et al.* 2010). In accordance with Beard (1949), Type 5 has a high presence of a *Opuntia* sp. in the herb layer and the presence of a *Cephalocereus* sp. Based on the dominance of *Pisonia fragrans* in Type 5 this type fits better with the 'Southern Island' form of this plant community (Beard 1944) and because of the dominance of *P. subcordata* Type 4 corresponds with the 'Leeward Island' form of the deciduous seasonal forest (Beard 1944).Type 4 fits a little bit better with the deciduous seasonal forest as described by Beard (1944) because of the significant presence of *Coccoloba swartzii*. Type 4 has a higher presence of the following characteristic species for the deciduous seasonal forest: *Bourreria succulenta, Tabebuia pallida, Citharexylum spinosum,* and *Erythroxylum* sp.

The Capparis-Gymnanthes type (Type 6) and Pisonia-Ayenia type (Type 8) do not fit any of the communities described by Stoffers (1956) for St. Eustatius. Type 6 (Capparis - Gymnanthes type) best resembles 'Woodland derived from evergreen forest' and is characterized by the fact that evergreen species are predominant over deciduous ones. This unit was however not described by Stoffers (1956) for St. Eustatius. Type 8 (Pisonia - Ayenia type) is a disturbed woodland type vegetation that is difficult to classify because its dominant tree species (Pisonia sucordata) and other significant covering tree species, (e.g. Citharexylum spinosum, Bourreria succulenta, Bursera simaruba, Capparis cynophallophora) occur in both deciduous seasonal forest and semi-evergreen seasonal forest (Stoffers 1956). Because Pisonia subcordata is deciduous, this would indicate some relationship with 'deciduous seasonal forest' but e.g. the absence of bromeliads (Stoffers 1956) obscures this relationship. This type also contains a high presence and cover of Bothriochloa pertusa an invasive grass species (Howard 1979) that was not present on the island during Stoffers' research (Stoffers 1956). This species is present in six other vegetation types on St. Eustatius.

5.3 Main land type

Stony rough land is the main land type in the areas of the present vegetation survey (Veenenbos 1955; see soil map). Four vegetation types (Type 1, 2, 6 and 7) do occur exclusively in this land type (Table 3). All have an evergreen character: type 1 belongs to the Seasonal formations and the other three types to the Dry evergreen formations. Three different soil types are described for this land type: the very shallow, gritty, stony clay soils of the northern part of St. Eustatius, the coarse sandy loam soils of the crater and crater rim of the Quill volcano and the gypsum-limestone slab of the White Wall (Westermann & Kiel 1961). The presence of the latter soil type is reflected in the exclusive occurrence of the *Antirhea - Dodonaea* type (Type 7) in the White Wall and Big Gut areas. Type 7 corresponds with Stoffers' (1956) Dry evergreen bushland (Table 5). Different from Stoffers (1956) is that the invasive grass species *Bothriochloa pertusa* occurs frequently and abundantly in the Type 7. This species was not present on St. Eustatius in the 1950s (Stoffers 1956).

In general 'Stony rough land' is unsuitable for cultivation while woodcutting seems to be a very difficult practice on its steep and very stony slopes (see also the Land capability map of St. Eustatius in Veenenbos 1955). That the level of disturbance would be relatively low in these areas (with the exception of the area in the crater of the Quill that was formerly cultivated: Stoffers 1956) is reflected in the presence of four primary climax communities (Types 1, 2, 3 and 7) in the Quill area: *Myrcia - Quararibea* type (Type 1), *Coccoloba - Ardisia* type (Type 2), *Chionanthus - Nectandra* type (Type 3) and the *Antirhea - Dodonaea* type (Type 7). In Type 1, big (old) trees and various species occurring exclusively in this type (especially ferns) are present. Type 2 has the most species of all the vegetation types of the island and also has a relatively rich epiphytic flora. Type 3 is the most widespread of these four vegetation types, and also includes big (old) trees. Type 7 occurs in two of the most inaccessible parts of St. Eustatius (for men but not for goats!).

5.4 Comparison of the vegetation map of Stoffers (1956) with that of the present study

Despite the difference in methodology used, a comparison is possible between our map and that of Stoffers (1956) based especially on the fact that both maps have the same scale (1:37,500). The comparison shows that there are some striking similarities but also important differences.

As in most Caribbean islands, the edaphic plant communities have suffered severely from human disturbance (see e.g. Johnson 1988; Debrot & De Freitas 1991; Debrot & Sybesma 2000). On St. Eustatius this is the case with the *Hippomane* woodland and the littoral woodland. In coastal areas, Stoffers (1956) found *Hippomane* woodland near Tumble Down Dick Bay and between Oranjestad and Gallows Bay. Today only very small (disturbed) fragments remain of this woodland (that were too small to be mapped in the present study). In the past *Hippomane*, known for its caustic sap was a special, difficult to work, light-colored wood used for heavy furniture. The small strip of littoral woodland along Venus Bay mapped by Stoffers (1956) can still be recognized and has improved judging from the increase in (average) height of the shrubby vegetation from 0.5 m (Stoffers 1956) to slightly above 1 m in the present study. From the map of Stoffers (1956) it can be concluded that the littoral woodland at Concordia bay at present is located at a more northwestern position. It seems to have diminished in surface area but is slightly higher or of approximately the same height and high coverage (*Coccoloba uvifera*) as in Stoffers (1956). However, today the area still shows strong signs of human disturbance and many cattle graze in the area. Also near Fort de Windt a littoral woodland occurs.

The maps in both studies show a relatively low variety of vegetation units in the area of The Mountains (three vegetation types in Stoffers (1956) and five in the present study). Both also show a high variety of legend units that follow a clear zonation from the less disturbed higher parts of the Quill down towards the more disturbed and species-poor vegetation types of the coastal areas and the Cultuurvlakte. The vegetations of these two main landscape units of St. Eustatius are very different. In The Mountains the total vegetated area became substantially less after the establishment of an oil terminal (Statia Terminals N.V.) in 1982 (De Palm 1985) which occupied about a fifth of this area at the time of the present survey. During Stoffers' study (Stoffers 1956) this area was still heavily affected by firewood harvest for charcoal production, but at present these activities do not take place anymore in the area. On the one hand there is deterioration: the area covered by woodland derived from forest intermediate between seasonal and dry evergreen has diminished and thorny woodland have been replaced by more degraded vegetation types. However, signs of improvement are also present: the lower abundance of Acacia spp., Leucaena leucocephala and Croton flavens. However, the presence of goats was noted in over 80 % of the plots and in most cases refers to the presence of goat dung in the plots. The following areas of The Mountains are protected by law (St. Eustatius Flora and Fauna Ordinance, AB 1997, No.06 & St. Eustatius Flora and Fauna Resolution, AB 1997, No. 07; DCNA 2008): Boven, Venus, Gilboa Hill,

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Bergje and Signal Hill. Persons that keep animals are responsible for the damage caused by animals to species protected by this law. These protected areas harbor landscape units H1, H2, Cliffs and the Venus Beach area. The combined protected area of the Mountains is about 3.47 km².

In accordance with Stoffers (1956), at the time of our study only a small part of the 'Cultuurvlakte' had a natural vegetation that was not totally disturbed and thus could be mapped. In Stoffers (1956) this area was mapped as a 'Thorny woodland derived from seasonal formations'. From the results in the present study it can be concluded that *Acacia spp.* play a much less significant role in this vegetation than as indicated by Stoffers (1956) and that the vegetation has more the character of a savannah vegetation with a variable composition of (a few) evergreen and deciduous tree species in the tree layer. The disturbance of the area is reflected in the significant presence of the invasive vine *Antigonon leptopus* (Arnoldo 1971; Langeland *et al.* 2008).

The exterior slope of the Quill has been declared a national park from a height upwards of 250m, as well as the inside walls of the crater and the vegetation on the crater floor, as well as White Wall down to sea level (St. Eustatius Flora and Fauna Ordinance, AB 1997, No.06 & St. Eustatius Flora and Fauna Resolution, AB 1997, No. 07; DCNA 2008). The following units of the present study fall into this national park: M1 (*Myrcia-Quararibea* Mountains), M2 (*Coccoloba-Chionanthus* Mountains), M3 (*Chionanthus-Nectandra* Mountains), M5 (*Pisonia-Eugenia* Mountains) and M8 (*Antirhea-Coccoloba* Mountains). The latter two types occur on the side of White Wall. In the Quill area no less than nine sub-landscapes (M1-M9) were recognized harboring four primary climax communities and six other vegetation types. Such diversity on a small, formerly heavily-used island is remarkable.

Two of the 'higher' climatic communities found on St. Eustatius (Montane thicket and Elfin woodland) by Stoffers (1956) were not found in the present vegetation study. The patch of Elfin woodland Stoffers (1956) formerly on the highest part of the rim on the south-eastern part of the Quill (Mazinga) was no longer present. Augustinus *et al.* (1985) implicate a brush fire as a likely cause for the disappearance of elfin woodland from the Quill. Indeed, in 1984 campers caused a fire on the western rim that burned for 3 weeks before it was finally put out by Dutch marines (M. Hoogland, pers. comm.). However, this was not an area identified as previously having elfin woodland. Hurricanes, general aridification and/or grazing may all have played a role in the loss of the narrow patch of elfin woodland that formerly occurred on the rim of the Quill. Goats were seen in the crater and on the rim of the Quill and can therefore cause erosion by lowering vegetation cover, species diversity and by trampling the vegetation (Debrot & de Freitas 1993). Exotic grazers impede bromeliads and orchids from growing on the ground or on the lower parts of trees (Debrot & de Freitas 1993; De Freitas & Rojer, in press). Half of the orchid species known to occur on St. Eustatius are terrestrial or lithophytic (Stenapa 2008).

Appendix 2 shows the hurricanes and tropical storms that have passed within 120 nautical miles from St. Eustatius since 1956. The elfin woodland is a very delicate system that is characterized by important limitations for (rapid) regeneration (Byrd & Weaver 1977). These characteristics include: a limited number of plant species compared to forests in lower elevations; reduced root respiration caused by saturated soils (one of the causes of the characteristic dwarfing); high winds, leaching of the soils combined with low temperatures, the very limited production of seeds by the climax species, the seeds of advanced successional stages almost universally seem to require the reactions of the previous stages for efficient germination, extensive root systems to provide stability in muddy, unstable soil that therefore impose large spaces between plants and colonization from seed by secondary species is (very) difficult. Because of its position on the rim it is also possible that it has received damage also from hurricanes thereby limiting its recovery or even changing other characteristics of the plant community (Brokaw & Walker 1991; Bellingham 1991). At present the characteristic gnarled form of the trees of the dominant *Clusia major* (Stoffers 1956) is not prominent. *Clusia major* is also not the dominant tree species in the area anymore (as it was in Stoffers, 1956) but *Ternstroemia peduncularis*, that was the

second most prominent tree species in the elfin woodland. The ground layer is not that well developed and *Begonia retusa* mentioned by Stoffers (1956) is not present anymore (H. Madden, pers. comm.). Studies are needed on possible restoration measures for this unique and threatened vegetation unit of the Lesser Antilles. On the highest part of rim of the Quill, Stoffers (1956) described a 'Dry evergreen forest'. In the present study the M2 landscape that is dominated by the corresponding vegetation type (Type 2), is found in the same area as the dry evergreen forest and occupies a relatively larger area.

With respect to the Montane thicket of Stoffers (1956) it can be said that only Type 2 in the present study shows some resemblance to it. They have e.g. Cordia sulcata, Myrtaceae and Piperaceae species in common. Because of the fact that Type 2 is dominant in landscape unit M2 it could be concluded that the area occupied by the montane thicket today is less compared to Stoffers (1956), but one has to take also into account that montane thicket and dry evergreen forest have a significant number of species in common (5 of the 12 high tree species, 2 of the 5 low tree and shrub species and 4 of the 5 ground layer species; Stoffers 1956). One of the typical features of this thicket, a dense herbaceous ground cover, may have disappeared because of grazing and trampling by goats (e.g. Debrot & De Freitas 1993; Kobayashi et al. 1997; Weaver & Chinea 2003) and natural succession (see e.g. Walker et al. 1996). Another factor to consider is also that one of the main damages caused by hurricanes and gales (!; see Meagher 1997) to vegetation is that they reduce the canopy cover. This in turn may result in damage and changes to the herb layer due to the drying effect of the sun on the microhabitat of the herb layer (Fernandez & Fetcher 1991; Brokaw & Walker 1991; Weaver & Chinea 2003). Because the Montane thicket on the Quill consists of relatively high trees (12-15 m; Stoffers 1956) this makes it more vulnerable to hurricane damage than vegetation with shorter trees (Brokaw & Walker 1991). In most cases damage due to hurricanes caused a radical change in the physical structure of forests (Brokaw & Walker 1991). Many broken-off branches and tipped-off trees were found in the present survey in areas on the higher eastern slope of the Quill area where Stoffers (1956) indicated the exclusive presence of a (high) Montane thicket. No research has been conducted on the effects of hurricane and gales damage to these forests. In the present study this thicket was not found as such, although Type 2 had some characteristics of the Montane ticket but shared a number of characteristics with the Dry evergreen forest of Stoffers (1956). On the lower slope in the area of the Montane thicket (Stoffers 1956), the height of the trees were significantly lower than the characteristic 12-15 m height described by Stoffers. Areas that are frequently hit by hurricanes (e.g. more exposed areas and not necessarily areas that are in the direct path of the hurricane) are prone to significant change in species composition. Also the height of the vegetation in those areas tends to become lower over time (Bellingham 1991). Therefore, a likely explanation for the disappearance of the Montane thicket is a failure to regenerate from the damage caused by past hurricanes due to reduced resilience caused by goat grazing and possibly also changed microhabitat due to the resulting openness of the vegetation, ensuing landslides due to rain (Walker et al. 1991; Kobayashi et al. 1997), (species dependent) mortality of seedlings due to the hurricane itself (Brokaw & Walker 1991), the ensuing prolonged drought (Walker et al. 1991), or a combination of factors. It must be said also that distinguishing between Montane thicket and Dry evergreen forest would be difficult after hurricane damage because of the many species these vegetations had in common (see Stoffers 1956).

Somewhat lower, but still on the higher slopes of the Quill, the map of Stoffers (1956) indicates the occurrence of four plant communities (deciduous seasonal forest, semi-evergreen seasonal forest, secondary woodland derived from seasonal formations and a relatively small area of dry evergreen bushland, a primary plant community only found in the area of White Wall), while in the present study only one landscape unit was distinguished in the area (M3: *Chionanthus - Nectandra* Mountains). The only vegetation type (Type 3) found in this unit corresponds with the semi-evergreen seasonal forest of Stoffers (1956). This indicates a higher presence of evergreen (lower) tree species in comparison to Stoffers (1956) and indicates a process of natural restoration because evergreen species grow slower in

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comparison to deciduous species. In the present study a high variant and a low variant of the M3 landscape type are distinguished. The high variant occurs more often on the north-western and western slopes of the Quill that is characterized by a distinct and high tree layer that on average is 4-5 m higher than the low variant.

Furthermore, lower on the Quill slopes a process of succession seems also to have taken place. On the map of Stoffers (1956) these slopes (that in the past were mostly farmland) are today almost completely covered by thorny woodland. On the present map three sub-landscapes occur in this area: 1) at the eastern side of the Quill the Capparis - Pisonia Mountains (M4), which has a predominantly dry evergreen character; 2) at the western and southern sides of the Quill the Pisonia - Eugenia Mountains (M5) that has a vegetation that corresponds with the deciduous seasonal forest; 3) at the southern side of the Quill the Pisonia - Antirhea Mountains (M7), which has a vegetation intermediate between deciduous and evergreen. Thorny species such as Randia aculeata, Solanum racemosum and cacti are of some importance only in the vegetation of M7. A more or less thorny vegetation is also found on the lowest eastern slopes bordering the cliff. This area was not mapped by Stoffers (1956) and is still in use as pasture land. The M5 area in the southern part of the Quill corresponds with the dry evergreen bushland of Stoffers (1956) and in which evergreen species play a relatively bigger role. The lower parts of the slope of the Quill in the northwestern part corresponds in the present study with the M9 unit. The vegetation of this unit can be described as a grassland with groups of scattered low shrubs consisting of thorny and non-thorny species. This landscape type is also found in 'Behind the Mountain' in Stoffers (1956), an area that he did not map possible due to heavy human disturbance at that time. These areas are still characterized by heavy anthropogenic disturbance (e.g. grazing by exotic mammal species).

Stoffers (1956) described an area with 'Vegetation of the rock pavement' between Soldiers Gut and Sugar Loaf and described this vegetation as being scanty, containing only *Strumpfia maritima*, a few small scrubs of *Coccoloba uvifera* and some *Urechites lutea*. The importance of *Strumpfia* has turned in favour of *C. uvifera*, *Ernodea littoralis*, and *Dodonaea* spp.

'Vegetation of the rocky slopes' can still be clearly distinguished on all three Dutch Windward Islands (St. Eustatius, Saba and St. Maarten). Stoffers (1956) describes this community as very variable in structure and composition, but does not mention specifically any of the occurrences on any of the islands. In the present study the Types 12 and 13 of the *Coccoloba-Bothriochloa Cliffs* correspond best with that community. The *Coccoloba-Bothriochloa Cliffs* landscape occurs in the coastal area almost all around St. Eustatius (with the exception of the coastal area to the west of the capital Oranjestad and the area between Zeelandia Bay and Bargine Bay).

5.5 Overall assessment and recommendations

An overall assessment of our comparison to the map by Stoffers indicates that over the last five decades various natural vegetations of St Eustatius have either shown (partial) recovery due to succession (increase of evergreen plant species) or partial deterioration or loss due a number of factors among which one or more of the following: industrial development, grazing by goats and other exotic mammals, impact of exotic plant species, human disturbance and severe weather (hurricanes, storms, gales). Garbage dumping and its effects have probably contributed to the disappearance of a beach vegetation (littoral woodland) at Concordia Bay (Bargine Bay). Most critical are the loss or degradation of the Elfin woodland, and Montane thicket. These areas are likely of special importance to rare and moisture-dependent plants (such as tree species that are exclusive to these units, ferns, mosses, orchids and bromeliads) but also to several rare bird species some of which may or may not still be present in very small numbers. These include birds such as the Scaly-breasted Thrasher, *Margarpos fuscus* and the Bridled Quail-dove, *Geotrygon mystacea*, in the Quill area (Voous 1983, Collier & Brown 2008). The

higher reaches of the Quill supports populations of eight of the range-restricted birds of the Lesser Antilles (Collier & Brown 2008). The Audubon's Shearwater, *Puffinus Iherminieri*, which formerly nested abundantly in the hills and cliffs of The Mountains (e.g. Tumble Down Dick Bay in the area where the oil terminal now stands) and other areas around the island (e.g. Gallows Bay). The species is known to nest in ravines and guts (e.g. on Saba) and may have potentially nested in other areas of St. Eustatius in the past. There are no recent confirmations for nesting of this species on St. Eustatius. Small numbers of White-tailed Tropicbird (*Phaeton lepturus*) birds have been documented nesting at White Wall (Collier & Brown 2009).

Parts of the natural areas of both The Mountains and the Quill are protected by law, but goats and other roaming livestock are omnipresent in all habitats and continue to have evident impacts on the vegetation. The St. Eustatius Flora and Fauna Ordinance (A.B. 1997, no. 6) only holds the owner of these exotic animals responsible in case they damage the protected plant species mentioned in the St. Eustatius Flora and Fauna Resolution (A.B. 1997, no. 7). These protected species only include orchids and the endemic Ipomoea sphenophylla. Aside from generally reducing the resilience of the vegetation to major disturbance, intensive impact in the herbaceous layers likely affects regeneration of rare hardwood species directly through selective predation and indirectly by overall desiccation and increased exposure to the elements. Goats have a broad diet in the region and species eaten include canopy, mid-canopy and understory species (Melendez-Ackerman et al. 2008). Vegetation degradation further also affects the competitive balance towards (unpalatable) (likely) invasive species such as Antigonon leptopus, and Leucaena leucocephala, which have expanded significantly or massively into natural habitat in the last 50 years. Not only is general vegetation degradation suggested as a problem to endangered breeding seabirds, but goats likely also directly trample nesting burrows of seabirds (Collier & Brown 2009). Consequently, priorities for nature conservation are to reduce grazer densities in all areas, protect the most sensitive vegetations using total grazer exclusion, and experimenting with methods to spur vegetation recovery, including erosion control, propagation of rare and endangered species and reforestation with indigenous species. It is also advised to have permanent plots established in areas of the most sensitive vegetations in order to better understand causal factors of short- and longer term changes.

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Quality Assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 57846-2009-AQ-NLD-RvA). This certificate is valid until 15 December 2012. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Environmental Division has NEN-AND-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 27 March 2013 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

Justification

Report C053/12
Project Number: 430.82020.04

The scientific quality of this report has been peer reviewed by a colleague scientist and the head of the department of IMARES.

Approved: W.J. van der Burg

senior researcher tropical botany / seed technology

Signature:

Date: 24 May, 2012

Approved: F.C. Groenendijk, MSc.

Head of Department

Signature:

Date: 18 June 2012

Appendix 1. Synoptic table of the vegetation types of St. Eustatius. Differentiating species are indicated in bold.

Vogotation type:	1	2	2	4	Е	6	0	9	7	10	12	11	12
Vegetation type:	2	2	<u>3</u> 9		5	4	8			5	13 10	11	5
Number of sample plots:	26.5	3 46.3			33.4	18.5	12	5	6 12.5	9.4	4.2	5 9.6	15.4
Average no. of species:	2.5	10.9	37.6 6.2	31.0 6.6	7.5	.9	6.5	20.2	4.3	6.4	3.3	6.9	4.3
Standard deviation:	2.5	10.9	0.2	0.0	7.3	.9	0.3	4.4	4.3	0.4	3.3	0.9	4.3
Differentiating species													
Piper medium	V (3)	-	_	-	_	_	_	_	-	_	_	_	_
Asplenium cristatum	V (2)	_	_	-	_	_	-	_	_	_	_	-	_
Quararibea turbinata	V (4)	-	_	_	_	_	-	_	-	_	_	-	
Theobroma cacao	111 (7)	-	_	-	_	_	_	_	-	_	_	_	_
Faramea occidentalis	111 (2)	-	_	_	_	_	-	_	-	_	_	_	
Hirtella triandra	III (5)	-	-	-	-	-	-	-	-	-	-	-	-
Ocotea spec.	V (3)	-	_	_	_	_	-	-	-	-	_	-	-
Polypodium phyllitidis	III (1)	_	_	_	_	_	-	-	_	-	-	-	-
Coccoloba venosa	III (4)	-	-	-	-		-	-	-	-	-	-	-
Ficus trigonata	III (2)	-	-	-	-	-	-	-	-	-	-	-	-
Psychotria spec.	V (3)	-	-	-	_	-	-	-	-	-	-	-	-
Picrasma excelsa	III (1)	-	-	-	-		-	-		-	-	-	-
Philodendron lingulatum	III (5)	-	-	-	-	-	-	-	-	-	-	-	-
Solanum lancifolium	-	IV (1)	-	-	-	-	-	-	-	-	-	-	-
Eupatorium macranthum	-	IV (2)	-	-	-	-	-	-	-	-	-	-	-
Melothria pendula	-	IV (2)	-	-	-	-	-	-	-	-	-	-	-
Lomariopsis sorbifolia	-	IV (3)	-	-	-	-	-	-	-	-	-	-	-
Clusia major	-	V (2)	-	-	-	-	-	-	-	-	-	-	-
Ardisia obovata	-	V (4)	I (1)	-	-	-	-	-	-	-	-	-	-
Byrsonima spicata	-	V (3)	I (3)	I (1)	-	-	-	-	-	-	-	-	-
Justicia sessilis	_	-	II (2)	III (2)	V (3)	-	III (3)	II (1)	-	I (1)	-	I (3)	
Lantana involucrata	-	-	I (1)	II (3)	I (1)	-	II (2)	IV (3)	II (2)	-	-	-	
Setaria rariflora	-	-	-	II (3)	V (3)	III (3)	I (3)	-	I (3)	-	-	-	I (3)
Morisonia americana	-	-	-	I (1)	IV (1)	-	-	-	-	-	-	-	
Piscidia carthagenensis	-	-	-	I (1)	IV (2)	II (4)	I (2)	-	I (1)	I (5)	-	-	
Gymnanthes lucida	-		-	-	I (1)	IV (2)	-	-	I (1)	-	-	-	_
Boerhavia spec.	-	-	-	-	I (1)	-	I (3)	III (2)	-	I (3)	I (1)	-	_
Achyranthes aspera	-	-	-	-	I (1)	-	I (3)	III (1)	-	-	I (1)	I (2)	I (2)
Sida cordifolia	-	-	-	-	-	-	I (1)	IV (3)	I (1)	-	-	II (1)	-
Ayenia insulaecola	-	-	-	-	-	-	IV (3)	-	-	-	-	-	I (2)
Sida glomerata	-	-	-	I (1)	-	-	I (2)	111 (2)	-	-	-	-	
Herissantia crispa	-	-	-	-	-	-	-	11 (2)	-	-	-	-	
Antirhea acutata	-	-	-	-	-	II (1)	-	-	IV (3)	-	-	-	
Dodonaea viscosa	-	-	-	-	-	-	-	-	111 (2)	-	-	-	-
Dodonaea elaeagnoides	-	-	-	-	-	-	-	-	III (4)	-	-	-	
Cyperaceae spec. 1	-	II (3)	-	II (3)	I (2)	-	-	-	I (2)	III (3)	-	I (3)	
Coccoloba uvifera	-	-	-	-	-	-	-	-	I (4)	-	V (6)	-	II (3)
Bouteloua americana	-	-	-	-	-	-	I (6)	-	I (3)	-	-	I (2)	III (2)
Desmodium triflorum	-	-	-	-	-	-	-	-	-	-	-	-	11 (2)

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Vegetation type:	1	2	3	4	5	6	8	9	7	10	13	11	12
Number of sample plots:	2	3	9	7	11	4	12	5	6	5	10	5	5
Average no. of species:	26.5	46.3	37.6	31.0	33.4	18.5	22.8	20.2	12.5	9.4	4.2	9.6	15.4
Standard deviation:	2.5	10.9	6.2	6.6	7.5	.9	6.5	4.4	4.3	6.4	3.3	6.9	4.3
Common species													
Maytenus laevigata	III (1)	V (2)	V (2)	III (3)	_	_	_	_	_		_	_	
Erythroxylum havanense	III (1)	IV (2)	V (3)	V (1)	III (2)	IV (2)	_	_	_		_		
Macfadyena unguis-cati	III (2)	IV (2)		III (3)		11 (3)	_		_		_		
Samyda dodecandra	III (2)	IV (1)	. ,	III (2)	` ,	IV (1)	I (1)	_	_	_	_		
Pisonia fragrans	III (1)	V (1)	IV (2)	11 (2)	V (2)	-	-	_	_		_		
Peperomia myrtifolia	III (4)	V (2)	IV (2)	II (3)	I (1)	_	_	_	_	_	_	_	_
Capparis indica	III (1)	- -	IV (1)	V (1)	II (1)	II (1)	II (1)	I (1)	_	_			
Tillandsia utriculata	V (2)	II (2)	II (1)			IV (3)	I (2)	- (1)	II (3)				
Cissus verticillata	V (2)	- -	V (2)	II (3)	I (2)	II (4)	-	<u>-</u>	-		I (2)		
Eugenia ligustrina	-	V (3)	V (2)	III (3)	IV (3)	-					1 (2)	-	
		V (3)		III (3)	IV (3)		I (1)						
Schoepfia schreberi Capparis cynophallophora	-		-	I (1)	III (1)	- V (4)	I (4)	- I (1)			<u>-</u>	<u>-</u>	<u>-</u>
Capparis cynophallophora Bursera simaruba		IV (1)	- IV (2)	IV (2)			I (4)	- (1)		-		-	-
		II (1)				III (3)			I (1)	-	-	-	-
Bourreria succulenta	-	IV (2)	II (1)	V (2)		III (1)	I (4)	-	I (1)		-	-	-
Citharexylum spinosum	-	IV (2)	V (3)	IV (1)	III (1)	11 (4)	11 (3)	-	-	11 (4)	-	-	-
Passiflora suberosa	-	V (3)	IV (2)	I (1)	I (1)	-	I (1)	-	-	-	I (1)		-
Coccoloba swartzii	-		III (3)		-	II (1)	- (0)	- (4)	II (1)		-		-
Antigonon leptopus	-	II (1)	-	-	-	-	1 (3)	I (1)	-	IV (8)	-	-	-
Randia aculeata	-	V (1)	V (2)	V (3)	V (2)	111 (3)	V (2)	V (2)	11 (2)	I (2)	-	I (1)	
Tabebuia heterophylla	-	V (1)	111 (2)	I (1)	-	II (1)	-	-	II (1)	-	-		1 (3)
Desmanthus virgatus	-	II (1)	I (1)	I (1)	-	-	I (1)	111 (2)	-	-	-	11 (2)	III (1)
Solanum racemosum	-	11 (2)	IV (1)	III (1)	V (2)	V (2)	IV (2)	I (1)	11 (2)	-		111 (2)	III (2)
Krugiodendron ferreum	-	-		IV (2)		IV (3)	-	-	-	-	-	-	-
Bidens cynapiifolia	-	-	II (1)	-	111 (2)	II (1)	I (1)	-	-	-	-	-	-
Abrus precatorius		-		111 (3)	I (2)	-	I (4)	-	-	I (2)	-	-	-
Capparis flexuosa		-	III (2)	V (1)	II (1)	III (3)	I (1)	-	-	-	I (1)	-	-
Heteropterys purpurea	-	-	III (2)	III (2)	V (2)	IV (2)	I (3)	-	-	I (1)	-	-	-
Pisonia subcordata	-	-		V (5)			IV (4)	I (1)	III (5)	-	-	-	-
Galacta dubia	-	-	I (1)	III (2)	III (3)	II (1)	I (1)	11 (3)	I (1)	-	-	-	-
Lantana camara	-	-	I (1)	II (1)	11 (2)	11 (2)	I (2)	I (2)	-	-	I (1)	-	-
Leucaena leucocephala	-	-	II (1)	III (2)	I (2)	11 (2)	II (2)	II (3)	I (2)	I (2)	I (2)	I (1)	-
Senna bicapsularis	-	-	II (1)	I (2)	III (2)	-	III (3)	-	-	-	I (1)	I (1)	-
Stigmaphyllon emarginatum		-	I (2)	V (2)	V (2)	-	IV (2)	-	I (2)	-	-	-	IV (2)
Commelina elegans	-	-	III (2)	IV (3)	V (3)	III (2)	11 (2)	I (2)	-	-	-	-	I (2)
Rauvolfia viridis	-	-	IV (1)	V (2)	V (1)	-	III (3)	V (3)	-	II (1)	-	11 (2)	I (3)
Acacia macracantha	-	-	II (4)	I (1)	II (1)	II (1)	II (2)	IV (2)	I (3)	-	I (1)	I (1)	I (3)
Comocladia dodonaea	-	-	-	III (1)	IV (1)	III (1)	I (1)	-	II (2)	-	-	-	-
Pilosocereus royeni	-	-	-	11 (2)	III (2)	11 (2)	III (1)	-	I (1)	-	-	-	-
Malpighia emarginata	-	-	-	I (1)	III (4)	II (6)	I (1)	I (2)	-	-	-	-	-
Sidastrum multiflorum	-	-	-	III (3)	III (2)	-	V (3)	IV (2)	-	-	-	-	-
Jatropha gossypiifolia	-	-	-	I (1)	II (1)	II (1)	IV (2)	IV (2)	-	IV (2)	-	V (3)	-
Croton astroites	-	-	-	III (1)	III (1)	II (1)	-	-	-	-	-	-	I (4)
Sida glabra	-	-	-	II (2)	II (2)	-	III (2)	-	-	I (3)	-	_	-

Vegetation type:	1	2	3	4	5	6	8	9	7	10	13	11	12
Number of sample plots:	2	3	9	7	11	4	12	5	6	5	10	5	5
Average no. of species:	26.5	46.3	37.6	31.0	33.4	18.5	22.8	20.2	12.5	9.4	4.2	9.6	15.4
Standard deviation:	2.5	10.9	6.2	6.6	7.5	.9	6.5	4.4	4.3	6.4	3.3	6.9	4.3
Tournefortia volubilis	-	-	-	11 (2)	II (2)	-	I (1)	-	-	-	-	I (1)	-
Centrosema virginianum	-	-	-	I (1)	-	-	I (2)	II (2)	-	-	-	I (2)	II (2)
Croton flavens	-	-	-	I (1)	II (1)	-	II (3)	I (4)	-	-	I (1)	-	II (2)
Paspalum laxum	-	-	-	-	-	11 (3)	I (3)	I (3)	III (3)	-	-	-	-
Portulaca oleracea	-	-	-	-	11 (2)	11 (2)	II (2)	II (2)	-	11 (2)	I (2)	-	III (3)
Clerodendrum aculeatum	-	-	-	-	I (1)	-	I (1)	I (1)	-	I (1)	11 (4)	-	-
Agave spec.	-	-	-	-	II (2)	-	II (4)	-	III (2)	-	-	I (4)	I (1)
Opuntia triacantha	-	-	-	-	V (2)	-	V (2)	-	-	I (2)	-	I (2)	I (1)
Melochia tomentosa	-	-	-	-	I (2)	-	IV (2)	II (2)	-	I (2)	-	11 (3)	V (2)
Ruellia tuberosa	-	-	-	-	11 (3)	-	II (3)	III (2)		I (2)	-	-	III (2)
Bothriochloa pertusa	-	-		-	I (3)	-	IV (3)	IV (6)		11 (3)	I (3)	V (6)	IV (5)
Waltheria indica	-	-		-	-		II (2)	II (3)			-	I (1)	I (2)
Aristida adscensionis	-	-	-	-	-	-	II (3)	I (2)	IV (3)	-	-	I (3)	I (3)
Acacia spec.	-	-	-	-	-	-	I (3)	I (2)	-	-	-	III (2)	II (4)
Stylosanthes hamata	-	-	-	-	-	-	II (1)	III (3)	-	-	-	I (3)	11 (2)
Spermacoce bahamensis	-	-	-	-	-	-	I (3)	-	III (3)	-	-	I (1)	II (2)
Other species (occurring i			or 5 wi	th low p	resence								
Hyperbaena domingensis	III (4)	11 (2)	-			-	-	-	-	-	-	-	
Peperomia magnoliifolia	III (2)	11 (3)	-	-	-	-	-	-	-	-	-	-	
Pisonia aculeata	III (1)	11 (3)		<u> </u>		-			-	-	-	-	
Casearia decandra Ocotea coriacea	V (2)	V (3)	V (3)								-	-	
Anthurium grandifolium	III (2)	IV (3)	V (4)							-	-		-
Catopsis floribunda	III (3)	IV (3)	I (1)										
Allophyllus racemosus	V (2)	IV (2)	III (2)										
Myrcia splendens	V (2)	IV (2)	III (2)										
Smilax guianensis	V (1)	IV (1)	II (1)			_	_						_
Pharus glaber	V (3)	IV (2)	I (1)				-						
Polypodium pectinatum	V (3)	IV (3)	II (3)	-	_	_	_	_	_	_	_	_	_
Elaphoglossum rigidum	V (2)	II (1)	I (1)	_	_	_	_	_	_	_	_	_	_
Celtis iguanaea	V (2)	-	11 (2)	_	I (2)	_	_	_	_	_	_	-	_
Myrcia citrifolia	-	V (4)	IV (3)	-	-	_	_	_	_	_	_	_	_
Epidendrum ciliare	_	IV (1)	-	I (2)	_	_	_	_	_	_	_	_	_
Spondias mombin	-	IV (1)	II (4)	-	-	_	_	_	_	_	-	_	_
Miconia laevigata	_		III (2)	_	-	_	-	_	_	_	_	-	-
Ficus citrifolia	-	IV (2)	I (1)	-	-	_	_	_	_	_	-	_	_
Pimenta racemosa	-	IV (3)	II (1)	-	-	_	-	_	_	_	-	-	-
Bernardia corensis	-	11 (2)	III (2)	-	I (2)	_	-	_	_	_	-	-	-
Eugenia axillaris	-	V (2)	IV (2)		-	_	-	_	_	_	-	-	-
Guettarda scabra	-	V (4)	III (2)		-	_	-	_	_	_	-	-	-
Chionanthus compacta	-	V (3)	V (4)	I (1)	-	_	-	_	_	_	-	-	-
Psychotria nervosa	-	V (2)	IV (3)		-	_	-	_	_	_	-	-	-
Panicum trichoides	-	V (2)	III (2)	I (1)	-	_	-	_	_	_	-	-	-
		` '		` /									

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Vegetation type:	1	2	3	4	5	6	8	9	7	10	13	11	12
Number of sample plots:	2	3	9	7	11	4	12	5	6	5	10	5	5
Average no. of species:	26.5	46.3	37.6	31.0	33.4	18.5	22.8	20.2	12.5	9.4	4.2	9.6	15.4
Standard deviation:	2.5	10.9	6.2	6.6	7.5	.9	6.5	4.4	4.3	6.4	3.3	6.9	4.3
Chiococca parvifolia	-	IV (2)	IV (2)	III (3)	-	-	-	-	-	-	-	-	-
Rivina humilis		II (1)	-	I (1)	I (2)	-	-	-	-	-	I (3)	-	-
Cucurbitaceae spec.	-	-	III (1)	-	-	-	-	-	-	-	-	-	-
Dalechampia scandens	-	-	I (1)	III (2)	-	-	-	-	-	-	-	-	-
Capparis baducca	-	-	III (2)	-	I (1)	-	-	-	-	-	-	-	-
Gyminda latifolia	-	-	II (1)	I (1)	-	-	-	-	-	-	-	-	-
Tragia volubilis	-	-	III (2)	III (3)	II (2)	-	-	-	-	-	-	-	-
Cordia nesophila	-	-	I (1)	I (1)	II (2)	-	I (1)	-	-	-	-	-	-
Desmodium incanum		-	I (1)	I (2)	-	-	-	I (3)	-	-	-	-	-
Teramnus labialis		-	I (1)	I (1)	-	-	I (2)	I (2)	-	-	-	-	-
Phyllanthus amarus		-	I (1)	-	I (1)	-	I (1)	-	-	I (1)	-	-	-
Triphasia trifolia	-	-	II (1)	I (1)	-	-	-	-	-	I (1)	-	-	-
Rhynchosia reticulata	-	-	II (2)	II (2)	-	-	-	-	-	-	I (2)	-	-
Phoradendron trinervium	-	-	I (1)	I (1)	I (2)	II (1)	-		-	-	-	-	-
Pithecellobium unguis-cati	-	-	I (2)	I (1)	-	II (4)	-	-	-	-	-	-	-
Metastelma grisebachianum	-	-	-	I (1)	-	II (1)	-	-	I (1)	-	-	-	-
Sideroxylon obovatum	-	-	-	I (1)	I (1)	III (3)	-		-	-	-	-	-
Celosia spec.	-	-	-	I (1)	II (3)	II (3)	-	-	-	-	-	-	-
Plumbago scandens		-	-	I (4)	I (3)	-	I (2)	I (2)	-	-	-	-	-
Crossopetalum rhacoma	-	-	-	III (1)	-	-	I (4)	-	IV (2)	-	-	-	-
Setaria setosa	-	-	-	I (3)	-	-	I (3)	I (3)	-	11 (3)	-	-	-
Pedilanthus tithymaloides	-	-	-	I (3)	II (1)	-	-	-	-	-	-	-	III (1)
Capparis hastata	-	-	-	-	III (2)	II (1)	-	I (1)	-	-	-	-	-
Kallstroemia pubescens	-	-	-	-	I (1)	-	I (2)	II (3)	-	I (2)	-	-	-
Boerhavia diffusa	-	-	-	-	II (2)	-	I (2)	I (1)	-	-	-	-	I (2)
Cuscuta spec.	-	-	-	-	I (1)	-	II (1)	-	-	-	-	-	I (1)
Melocactus intortus	-	-	-	-	I (1)	-	I (1)	-	-	-	I (1)	-	II (2)
Sida ciliaris	-	-	-	-	I (1)	-	-	-	-	-	-	I (3)	II (1)
Annona squamosa	-	-	-	-	-	-	I (4)	-	-	II (2)	-	-	-
Urechites lutea	-	-	-	-	-	-	III (2)	I (1)	-	-	-	-	-
Desmodium procumbens	-	-	-	-	-	-	I (1)	I (2)	-	-	-	I (2)	II (3)
Jacquinia armillaris		-	-	-	-	-	-	-	I (1)	-	I (3)	-	I (3)
Tragus berteronianus	-		-	-	-	-	-	-	-	II (5)	-	-	III (3)
Rare species													
Schaefferia frutescens	-	-	-	-	II (1)	-	-	-	-	-	-	-	
Peperomia humilis	-	-	-	-	II (1)	-	-	-	-	-	-	-	-
Cyperaceae spec. 2	-	-			-	-	-	-		II (3)			
Croton betulinus	-	-			-	-	-	II (3)			-	I (2)	
Heliotropium angiospermum	-	-	-	-	-	-	II (1)	-	-	-	-	I (1)	-
Hylocereus trigonus	-	-	-	-	-	II (1)	-	-	-		-	-	-
Andira inermis	-	II (1)	-		-	-	-	-	_				
Psilotum nudum	-	II (1)						-		-		-	
Solanum americanum	-	II (1)	-	-	-	-	-	-	-		-	-	-

Vegetation type:	11	2	3	4	5	6	8	9	7	10	13	11	12
Number of sample plots:	2	3	9	7	11	4	12	5	6	5	10	5	5
Average no. of species:	26.5	46.3	37.6	31.0	33.4	18.5	22.8	20.2	12.5	9.4	4.2	9.6	15.4
Standard deviation:	2.5	10.9	6.2	6.6	7.5	.9	6.5	4.4	4.3	6.4	3.3	6.9	4.3
Tabernaemontana citrifolia	-	II (1)	-	-	-	-	-	-	-	-	-	-	
Zanthoxylum flavum	-	II (1)	-	-	-	-	-	-	-	-	-	-	-
Cestrum laurifolium	-	11 (2)	-	-	-	-	-	-	-	-	-	-	-
Pitcairnia angustifolia	-	11 (2)	-	-	-	-	-	-	-	-	-	-	-
Peperomia glabella	-	II (3)	-	-	-	-	-	-	-	-	-	-	
Urticaceae spec.	-	II (3)	-	-	-	-	-	-	-	-	-	-	-
Vernonia cinerea	-	II (3)	-	-	-	-	-	-	-	-	-	-	
Vittaria lineata	-	II (3)	-	-	-	-	-	-	-	-	-	-	
Ternstroemia peduncularis	-	II (4)	-	-	-	-	-	-	-	-	-	-	-
Inga laurina	-	II (1)	II (3)	-	-	-	-	-	-	-	-	-	-
Zanthoxylum martinicense	-	II (1)	II (1)	-	-	-	-	-	-	-	-	-	-
Ocotea patens	-	II (1)	II (3)	-	-		-	-	-		-	-	
Pavonia spinifex	-	-	II (2)	-	-	-	-	-	-	-	-	-	
Polypodium heterophyllum		-	II (3)				-						
Ceiba pentandra	-	-	II (1)	-	-	-	-	-	-	-	-	-	-
Melicoccus bijugatus	-	-	II (3)	I (1)	-	_	_	-	-	_	-	_	_
Capparis linearis		-	I (1)	-	_	_	_	-	_	_	_	_	_
Physalis angulata		-	I (2)	_	I (2)	_	_	-	_	_	_	_	_
Eugenia monticola		_	I (1)	-	-	_	_	-	_	_	_	_	_
Polypodium lycopodioides		_	I (3)	_	_	_	_	_	_	_	_	_	_
Pilea semidentata		_	I (3)	_	_	_	_	_	_	_	_	_	_
Justicia eustachiana		_	I (3)	_	_	_	_	_	_	_	_	_	
Eugenia uniflora		_	I (1)			_				_		_	
Aristida spec.		_	I (3)			_				_		_	
Passiflora laurifolia		_	I (1)					_					
Daphnopsis americana		_	I (1)										
Piper dilatatum			I (1)										
Exothea paniculata			I (4)		-								
Zanthoxylum punctatum		-	I (1) I (1)	- 1 (1)			-	<u>-</u>			<u>-</u>		
Ipomoea tiliacea		-		I (1)			-			-			-
Sida abutifolia		-	-	I (1)	-		-	-					
Tillandsia recurvata		-	-	I (1)	-	-	-	-	-	-	-	-	
Asparagus spec.		-	-	I (1)	-	-	-	-	-	-	-	-	
Caesalpinia bonduc		-	-	1 (2)	-	-	-	-	-	-	-	-	
Annona muricata		-	-	I (1)	-	-	-	-	-	-	-	-	-
Triumfetta semitriloba		-	-	I (1)	-		-	-	-		-	-	
Cyperus distans		-	I (3)	-	-	-	I (1)	-	-	-	-	-	
Abutilon umbellatum		-	-	-	I (3)	-	-	-	-	-	-	-	
Amaranthus polygonoides		-	-	-	I (1)	-	-	-	-	-	-	-	
Cheilanthes microphylla		-	-	-	I (3)	-	-	-	-	-	-	-	-
Chloris inflata		-	-	-	I (3)	-	I (3)	-	-	-	-	-	-
Chloris virgata		-	-	-	I (3)	-	-	-	-	-	-	-	I (2)
Cissampelos pareira		-	-	-	I (3)	-	-	-	-	-	-	-	
Melochia pyramidata		-	-	-	I (1)	-	-	-	-	-	-	-	-

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Vegetation type:	1	2	3	4	5	6	8	9	7	10	13	11	12
Number of sample plots:	2	3	9	7	11	4	12	5	6	5	10	5	5
Average no. of species:	26.5	46.3	37.6	31.0	33.4	18.5	22.8	20.2	12.5	9.4	4.2	9.6	15.4
Standard deviation:	2.5	10.9	6.2	6.6	7.5	.9	6.5	4.4	4.3	6.4	3.3	6.9	4.3
Talinum fruticosum		-	-	-	I (2)	-	-	-	-	-	-	-	
Turnera ulmifolia		-	-	-	I (1)	-	-	-	-	-	-	-	-
Amyris elemifera		-	-	-	I (1)	-	-	-	-	-	-	-	
Guettarda odorata		-	-	-	I (1)	-	-	-	-	-	-	-	-
Ipomoea sphenophylla		-	-	-	I (2)	-	-	-	-	-	-	-	-
Chiococca alba		-	-	-	I (1)	-	-	-	-	-	-	-	-
Malvaceae spec.		-	-	-	I (1)	-	-	-	-	-	-	-	
Metastelma spec.		-	-	-	I (1)	-	-	-	-	-	-	-	
Eugenia cordata		-	-	I (4)	I (1)	-	-	-	-	-	-	-	-
Abutilon spec.		-	-	-	I (2)	-	-	-	-	-	-	-	-
Wedelia spec.		-	-	-	I (1)		-	-	-	-	-	-	-
Sesuvium portulacastrum		-	-	-	I (2)		-	-	-	-	-	-	
Poaceae spec.		-	-	-	I (3)	-	I (3)	-	-	-	-	-	-
Wedelia calycina		-	-	-	I (2)	-	-	-	I (1)	-	-	-	-
Amaranthus dubius		-	-	-	I (1)	-	I (1)	-	-	-	-	-	-
Cracca caribaea		-	-	-	I (3)	-	I (2)	-	-	-	-	-	-
Lantana urticifolia		-	-	-	I (1)	-	I (3)	-	-	-	-	-	-
Cyperus elegans		-	-	-	-	-	-	-	I (3)	-	-	-	-
Erithalis fruticosa		-	-	-	-	-	-	-	I (1)	-	-	-	-
Eupatorium odoratum		-	-	-		-		-	I (1)	-	-	-	-
Strumpfia maritima		-	-	-	-	-	-	-	I (2)	-	-	-	-
Paspalum spec.		-	-	-	-	-	-	-	I (3)	-	-	-	-
Coccoloba spec.		-	-	-		-		-	I (1)	-	-	-	-
Cyperaceae spec. 3		-	-	-		-		-	I (3)	-	-	-	-
Portulaca halimoides		-	-	-	I (1)	-	-	-	-	I (2)	-	-	-
Ernodea littoralis		-	-	-		-		-	I (2)	-	I (5)	-	-
Amaranthus crassipes		-	-	-		-	I (1)	-	-	-	-	-	-
Euphorbia spec.		-	-	-	-	-	I (2)	-	-	-	-	-	-
Sida jamaicensis		-	-	-		-	I (2)	-	-	-	-	-	-
Stachytarpheta jamaicensis		-	-	-		-	I (1)	-	-	-	-	-	-
Kallstroemia spec.		-	-	-		-	I (3)	-	-	-	-	-	-
Clerodendrum aculeatum		-	-	-	-	-	I (4)	-	-	-	-	-	-
Verbenaceae spec.		-	-	-	-	-	I (2)	-	-	-	-	-	-
Eragrostis spec.		-	-	-	-	-	I (3)	-	-	-	-	-	-
Boerhavia erecta		-	-	-			I (1)	-	-	-	-	-	-
Tecoma stans		-	-	-	-	-	I (1)	-	-	-	-	-	-
Malvaceae spec.		-	-	-	-	-	I (3)	-	-	-	-	-	-
Pilea microphylla		-	-	-	I (2)		-	-	-	-	-	I (2)	-
Acalypha poiretti		-		-			I (2)		-	I (2)		-	
Physalis pubescens		-	-	-	I (2)	-	-	-	-	-	-	-	I (1)
Corchorus aestuans		-	-	-	-	-	I (1)	I (2)	-	-	-	-	-
Paspalum bakeri		-	-		-	-	-	-	I (3)	-	-	-	I (1)
Malvastrum americanum		-	_	-	_	_	-	-	-	I (1)	-	-	
Mollugo verticillata		-	-	-	-	-	-	-	-	I (1)	-	-	-
										· · /			

Vegetation type:	1	2	3	4	5	6	8	9	7	10	13	11	12
Number of sample plots:	2	3	9	7	11	4	12	5	6	5	10	5	5
Average no. of species:	26.5	46.3	37.6	31.0	33.4	18.5	22.8	20.2	12.5	9.4	4.2	9.6	15.4
Standard deviation:	2.5	10.9	6.2	6.6	7.5	.9	6.5	4.4	4.3	6.4	3.3	6.9	4.3
Cyperus amabilis		-	-	-	-	-	-	I (2)	-	I (3)	-	-	-
Spermacoce assurgens		-	-	-	-	-	-	I (2)	-	-	-	-	
Portulaca quadrifida		-	-	-	-	-	-	I (4)	-	-	-	-	
Conocarpus erectus		-		-			-		-	-	I (8)	-	-
Hippomane mancinella		-		-		-	-		-	-	I (4)	-	
Sporobolus virginicus		-	-	-	-	-	-	-	-	-	I (3)	-	-
Thespesia populnea		-	-	-	-	-	-	-	-	-	I (9)	-	
Abutilon indicum		-		-	I (2)	-	-		-	-	I (2)	-	
Priva lappulacea		-		-			-		-	-	I (1)	-	
Pappophorum pappiferum		-	-	-	-	-	I (3)	-	-	-	-	-	I (1)
Anthephora hermaphrodita		-		-		-	-	I (3)	-	-	-	-	I (3)
Boerhavia coccinea		-		-			-		-	-	-	I (1)	-
Catharanthus roseus		-	-	-	-	-	-	-	-	-	-	I (2)	-
Boerhavia scandens		-	-	-	-	-	-	-	-	-	-	I (2)	-
Agave sisalana		-	-	-	-	-	-	-	-	-	-	-	I (1)
Lithophila muscoides		-	-	-	-	-	-	-	-	-	-	-	I (1)
Lantana spec.		-	-	-	-	-	-	-	-	-	-	-	I (1)
Portulaca grandiflora		-	-	-	-	-	-	-	-	-	-	-	I (2)
Desmodium spec.		-	-	-	-	_	-	_	-	-	-	-	I (1)
Explanation:													
- = species not present	in that v	voqetatio	n tyne										
+ = species present in 1				ts of the	at vogo	tation to	/DO						
I = species present in 6													
II = species present in 2													
III = species present in 4													
IV = species present in 61													
V = species present in 81-							<u> </u>						
Numbers between brackets in								ıhlicatio	า				
Nambers between brackets in	idicate	cover ca	regunes	Schiali	icu cisc	VVIICICI	ii tile pt	Joneallo	Tr.				

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Appendix 2. Monthly and annual average meteorological parameters for St. Eustatius, 1971-2000. (Courtesy of the Meteorological Service of the Netherlands Antilles and Aruba)

	METEO CURAÇÃO													
ORANJESTAD, ST. EUST	ATIUS	(17°29'	N, 62°5	9 'W)	SUMMA	ARY OF	CLIM	ATOLO	GICAL	DATA,	PERIO	D 1971	- 2000	
ELEMENT		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
Av. Air temperature	°C	25.3	25.2	25.5	26.2	27.1	27.9	28.0	28.1	27.9	27.4	26.6	25.5	26.9
Av. Maximum temperature	e °C	28.3	28.4	28.8	29.4	30.1	30.8	31.1	31.2	31.0	30.6	29.8	28.7	29.8
Abs. Maximum temperatur	re °C	31.0	31.3	31.7	33.1	32.9	33.5	33.6	33.9	33.7	34.3	33.5	31.4	34.3
Av. Minimum temperature	°C	22.5	22.3	22.7	23.3	24.1	25.0	24.9	25.0	24.7	24.4	23.7	23.1	23.8
Abs. Minimum temperature	e °C	19.0	18.9	18.4	19.4	19.1	21.6	21.0	21.0	21.0	18.8	19.3	18.7	18.4
Av. Air pressure (-1000)	hpa	16.8	17.3	17.2	16.2	16.8	17.4	17.4	15.9	14.4	14.1	14.0	16.2	16.1
Av. Vapour pressure	hpa	25.6	24.5	25.3	26.3	28.3	30.2	29.2	30.6	30.9	29.5	27.9	27.3	28.0
Av. Relative humidity	%	79.6	77.0	75.4	77.9	80.1	79.8	76.7	80.1	81.7	82.7	81.3	82.2	79.4
Av. Dewpoint temperature	°C	21.4	20.7	21.2	22.3	23.5	24.2	23.9	24.5	24.5	24.2	23.2	22.5	23.0
Av. Monthly rainfall	mm	52.0	50.5	48.8	55.7	87.1	60.6	74.1	106.9	123.2	106.5	128.6	74.6	985.8
Av. Days with rain	≥ 1,0	11.1	8.9	7.6	7.4	9.5	7.4	11.2	12.1	12.2	11.2	13.3	12.6	125.4
Highest rainfall in 24 hours	š	45.5	111.2	113.4	172.4	133.1	123.5	88.0	111.0	125.0	126.2	183.6	71.4	250.7
Av. Wind speed (10m)	m/s	5.1	4.6	5.4	4.8	4.4	5.2	5.7	5.1	4.2	3.9	4.6	5.2	4.8
Av. Maximum wind speed	m/s	11.1	11.6	11.2	11.0	10.2	11.3	12.2	11.3	10.8	10.6	11.2	11.7	11.2
Strongest gust	m/s	18.9	18.4	18.4	15.8	14.8	18.9	25.5	21.9	21.9	26.5	19.9	18.9	25.5

Appendix 3. Hurricanes passing within 222 km from St. Eustatius in the period 1956-1999.

Hurricanes passing within 222 km from St. Eustatius in the period 1956-1999. Only hurricanes or tropical storms with maximum sustained surface wind speed (1 minute mean; msswp) of minimally 50 mph near the Dutch Windward Islands (St. Eustatius, Saba and St. Maarten) are listed. Hurricanes that caused considerable damage to the Dutch Windward Islands are marked with an *.

Year	Month / day	Name hurricane	Msswp (mph)
1956	9-aug	Betsy	90
1959	17-aug	Edith	50
1960	29-aug	Donna	145*
1963	25-okt	Helena	50
1964	20-aug	Cleo	100
1965	27-aug	Betsy	55
1966	21-sep	Inez	130
1975	14-sep	Eloise	td¹
1979	29-aug	Frederic	75¹
1989	10-sep	Hugo	140*
1990	3-okt	Klaus	75
1995	22-aug	Iris	65
1995	27-aug	Luis	65*
1995	12-sep	Marilyn	95*
1996	5-jul	Bertha	80
1998	15-sep	Georges	100
1999	17-okt	Jose	75*
1999	13-nov	Lenny	115*

^{*} ts= tropical storm; td= tropical depression.

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¹ These two events caused prolonged extensive flooding because of their associated torrential rainfall of more than 250 mm. Source: Meterological Department Curação (2011).

Appendix 4. New plant names

Newer plant names (as by Axelrod 2011) for species treated in the text using older nomenclature sources (as listed in the Methods section).

Genus r	name	Species name					
was	is	was	is				
Acacia	Valchellia	macracantha					
	vaicrieilia		indica				
Acalypha Abutilon	Pseudabutilon	poiretti umbellatum	IIIUICa				
			agutatum				
Antirhea Boerhavia	Stenostomum	acutata	acutatum				
	Commicarpus	scandens					
Caesalpinia	Guilandina	bonduc , ,	6 1				
Capparis	Capparidastrum	baducca 	frondosum				
Capparis	Quaderella	cyanophallophora	1				
Capparis	Cynophalla	flexuosa					
Capparis	Cynophalla	hastata					
Capparis	Quaderella	indica					
Cestrum		laurifolium	citrifolium				
Chiococca		parvifolia	alba				
Chionanthus		compacta	compactus				
Chloris		inflata	barbata				
Clerodendrum	Volkameria	aculeatum	aculeata				
Commelina		elegans	erecta				
Cracca	Coursetia	caribaea					
Erythroxylum	Erythroxylon	havanense					
Eupatorium	Chromolaena	macracanthum					
Eupatorium	Chromolaena	odoratum	odorata				
Galacta	Galactia	dubia					
Jacquinia		armillaris	arborea				
Lanatana		urticifolia	camara				
Ocotea	Nectandra	coriacea					
Ocotea	Nectandra	patens					
Opuntia		triacantha	triacanthos				
Pharus		glaber	lapulaceus				
Pilocereus		royeni	royenii				
Pisonia	Guapira	fragrans	_				
Polypodium	Microgramma	heterophyllum	heterophylla				
Polypodium	Microgramma	lycopodioides					
Polypodium	Plecuma	pectinatum					
Polypodium	Campyloneurum	, phyllitidis					
Setaria		rariflora	setosa				

Solanum		racemosum	bahamense
Spermacoce		assurgens	remota
Urechites	Pentalinon	lutea	luteus
Vernonia	Cyanthillium	cinerea	cinereum

