Diversity and dynamics of the vegetation on the sandstone plateaus of the Colombian Amazonia
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Objectives

This actuo- and paleo-ecological study has two interrelated objectives. First, it aims at documenting the diversity of vegetation types occurring on the sandstone plateaus in the Colombian Amazon. This is done by vegetation relevés and subsequent phytosociological analysis. Second, it aims at understanding the recent vegetation development on the Araracuara’s sandstone formation by using a very detailed pollen record, modern pollen rain and information from the vegetation survey.

Vegetation on West Guayan sandstone plateaus of the Middle Caquetá region, in the Colombian Amazonia

The vegetation of the sandstone plateaus of the region of the Middle Caquetá river includes a large number of herbaceous monocotyledonous families, mostly Bromeliaceae, Cyperaceae, Eriocaulaceae en Xyridaceae and also shrubby dicotyledonous species, most of which are small in size, frail and sclerophyllous. A phytosociological survey (using TWINSPAN computer package) was carried out on 346 vegetation relevés, distributed over four general vegetation covers developing on the hard rock and white sand substrates: pioneer vegetation (lichens, mosses and small herbs), herbaceous vegetation, shrubland and low forest, on six sandstone plateaus. This resulted in the identification of twenty-three main vegetation types. In the pioneer and herbaceous vegetation, one community and seventeen associations were recognized: Clusio chiribiquetensis-Navietum garcia-barrigae, Axonopodo schultesii-Navietum garcia-barrigae, Pachiro coriaceae-Axonopodetum schultesi, Syngonantho humboldtii-Paspaletum tillettii, Syngonantho vaupesamum-Yxridetum wurdackii, Xyrido wurdackii-Paspaletum tillettii, Siphanhero hostmannii-Yxridetum paroens, Xyris mina-Lagenocarpus verticillus, Syngonantho humboldtii-Panietum orinocanum, Xyrido longophyllae-Paspaletum tillettii, Sturnugesis fruticosaceae-Brocchinietum hechtioides, Axonopodo schultesii-Schoenoephalietum martianae, Bulbostylido lamiae-Blychsenoporetum globosae, Burmannia bicoloris-Monotremetum xyridioides, Schoenoephalo martianum-Orateetum roraimae, Epipacto parviflorum-Crotonea turn, L'tricularietum neottioidis, Tepuiantho colombiani-Euceraeetum nitidi, Ocotea esmeraldanae-Clisetum opaca, Everardio montanae-Bonnetietum martianae, Brocchinio hechtioides-Bonnetietum martianae and Macaireo rufescensis-Bonnetietum martianae. A floristic characterization of each association is provided, as well as information about its ecology and distribution. The variation in composition and extension of each association is strongly related to the degree of humidity, desiccation and/or to the lacking soil formation.

Plant species compositional patterns.

Vascular plant species compositional patterns of vegetation on white sand soils and sandstone substrates were studied at six sandstone plateaus in Colombian Amazonia, by means of a field survey according to the Braun-Blanquet relevé method. Canonical correspondence analyses (CCA) were applied to separate effects of habitat and spatial configurations of the plateaus on species patterns. Also, information of dispersal ability and phytogeographic affinity of species was used to test explanations for between-plateau differences. The link of species to the spatial configurations of the sandstone plateaus was determined by means of a t-value biplot procedure in CCA.

A total of 208 species were recorded in 212 relevés. The main gradients in the species patterns were linked to the spatial configuration of the plateaus. Spatially controlled species patterns were mainly related to soil depth and soil carbon content. The association between phytogeographic affinity and the habitat-controlled spatial link of species pointed at insufficient sampling at one plateau. Dispersal ability did not explain the habitat-controlled spatially distributed occurrences of plant species. This would point at a low frequency of local extinction at the sandstone plateaus, especially of the poorly dispersed species. Extended plant longevity might help plants to bridge unfavourable periods related to fire or temporary droughts. Space- and habitat-controlled species patterns at one plateau were quite distinct from patterns at and between the other plateaus. This might be due to unmeasured habitat factors (e.g. unrecorded soil variation or human disturbance history) or the preferential, surveyor-biased sampling procedure.

Phytogeographic analysis of vascular species.

The vegetation of the sandstone plateaus of the Colombian Amazonia (at altitudes below 350 m. alt.) includes pioneer, herbaceous, shrub and low forest vegetation types. The preliminary checklist of these formations includes 381 species of vascular plants, which belong to 205 genera and 77 families. The families with the highest number of species are Cyperaceae (28), Orchidaceae (24), Melastomataceae (22), Xyridaceae (22), Rubiaceae (21), Bromeliaceae (16), Apocynaceae (15) and Poaceae (15); 34% of the families were represented by one species only. The genera with the
Summary

The highest number of species are *Xyris*, *Rhynchospora*, *Lindorea*, *Syngonanthus*, *Clusia*, *Mandevilla*, *Epidendrum*, *Abolboda*, *Croton*, *Miconia* and *Utricularia*.

To 302 of the Guayan shield species of Colombia a phytogeographical distribution could be assigned. 38.3% of these had a strict Guayan distribution (including 5.9% being endemic to the Colombian Guayan region) and 13.2% had an wider Amazonian distribution. A small percentage of the sandstone plateau species (4.6%) had a disjunctive distribution with the Brazil shield and 2.3% with the Andes-Chocó region. Less than half of all species had a wide distribution (37.6% neotropical and 3.9% pantropical). Eighteen species, including six species that were newly found in this study, are endemic to the Guaya Colombiana. The inclusion of the sandstone plateaus of the Middle Caquetá region in the western Guaya region confirms the presence of two endemic families and fifteen endemic genera in this region.

Seed dispersal modes of the vascular vegetation.

Dispersion spectra of the vascular flora of the sandstone plateaus were determined through characterization of the morphology of the dispersion units (seeds and fruits), their dispersion vectors and the fruiting events throughout the year. Dispersion spectra could be assigned to 294 species. The types of fruits reflect the dispersal mechanisms. There is a great variety of fruit types, from which capsules are the most abundant (44.3%), followed by berries (16.8%) and the fleshy drupes (15.1%). Abiotic dispersion (anemochory and autochory) were the most important dissemination mechanisms (49.8%), followed by dispersion by animals (zoochory; 46.6% of all species), while dispersal by water almost never occurs (hydrochory; 3.6%). For the zoochorous plants, birds are largest groups of potential dispersion vector (47.3%). These results contrast to the situation in the surrounding rain forest, where zoochoria is by far the main mechanism of dispersion and abiotic dispersion almost does not occur. Our results show that long distance dispersal is a dominant characteristic of the sandstone plateaus, since most of the species are bird and wind dispersed. The insular character of the sandstone plateaus can be discussed based on the theory of MacArthur and Wilson (1967) who predict long distance dispersal for the flora of biogeographic islands.

A palynological reconnaissance of latest Holocene vegetation change on the sandstone plateau of Araracuara.

The results of a study of a sediment profile and of modern pollen rain on a sandstone plateau near Araracuara and their relation with actual vegetation are presented. The floral composition of the vegetation on the sandstone plateau was studied on the basis of vegetation relevés. Comparing these data with modern pollen rain of 18 moss samples collected in different vegetation types, while using the association index of Davis (1984) and correspondence analysis, we evaluated to which degree pollen spectra reflect the actual vegetation. Rain forest taxa appeared overrepresented in the pollen rain on the sandstone plateau. Poaceae, Xyris, Cyperaceae and Melastomataceae showed highest correspondence between pollen rain and measured vegetation cover, whereas *Bonnetia*, Bromeliaceae, and Ochnaceae showed an intermediate level of accuracy.

Pollen analysis of a 25-cm sediment core, reflecting vegetation change on the Araracuara sandstone plateau during the last century, showed a transition from open Rapateaceae-dominated vegetation to a *Bonnetia martiana*-dominated scrub. Successional stages in the pollen record were interpreted as discrete vegetation communities in the field, all occurring at present day as part of a mosaic-like vegetation. The Δ13C values of the radiocarbon-dated samples suggested that there was a significant contribution of C4/CAM plants to the local vegetation. This is substantiated by the pollen record, which included a significant number of genera and families in which C4 and CAM physiological pathways are common.

General conclusions

In general, this study showed that the vegetation of the sandstone plateaus in Colombian Amazonia forms an example of a highly specialized flora to extreme environmental conditions. The sandstone plateaus form an ecosystem with an insular character within the Amazon rainforest. The typical characteristics of the vegetation (highly adapted to poor conditions, fragmented patches, etc.) make them a very fragile ecosystem to human impact like burning and airstrip development. This is why attention should be drawn to preserve intact examples of sandstone plateau formations, putting emphases on connectivity among them. The participation of local communities in the sustainable management of these habitats is of fundamental importance, considering their use for gathering activities symbolic and mythological values.