



Humus profiles and successional development in a rock savanna (Nouragues inselberg, French Guiana): A micro-morphological approach infers fire as a disturbance event

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Summary

The common development of vegetation and soil is a central issue in plant succession. We hypothesized that areas of woody vegetation decay and accumulation on the ground (zones of destruction or 'micro-chablis') played a role in the successional development of vegetation patches on tropical inselbergs and that disturbance events could be inferred from the analysis of the organic matter accumulated along a successional gradient. The study was conducted in French Guiana (South America). Nine humus profiles (each comprised of a varying number of layers) were selected in shrub thickets (~1 acre each) representative of three vegetation types of the rock savanna: canopies of pure *Clusia minor* (Clusiaceae), *C. minor* in mixture with *Myrcia saxatilis* (Myrtaceae) and zones of destruction. Using a dissecting microscope, a count point optical method for small soil volumes was employed to measure the volume ratio of each kind of humus component (107 categories) in the 62 layers sampled. Micro-morphological data were analysed by correspondence analysis (CA). Humus profiles varied with canopy tree type and revealed traits of past as well as trends for future plant succession. The lack of OL and OF horizons, and the presence of charred material differentiated the zones of destruction from other humus profiles and confirms the impact of spatially limited fires or lightning strikes in the cyclic development of vegetation patches.

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Introduction

Humus results from the biochemical transformation of residual vegetation by decomposer food-webs (Wolters et al., 2000). The direct observation of the soil under the microscope, also called micromorphology, was developed by Kubiëna (1938) and has proven to be essential for gaining knowledge of biological processes in surface horizons (Bernier, 1996). Humus forms therefore deserve special attention in studies of plant succession (Emmer and Sevink, 1993; Ponge et al., 1998). Historical characteristics and trends for future succession at the scale of years to decades can be derived from the observation of successive horizons by quantitative optical methods (Bernier and Ponge, 1994; Gillet and Ponge, 2002) and comparisons can be made among humus profiles by means of multivariate analysis (Peltier et al., 2001).

Tropical inselbergs are granite or sandstone outcrops which rise abruptly from the surrounding rain forest (Bremer and Sander, 2000) and support a special type of vegetation adapted to harsh and strongly varying environmental conditions. On the Nouragues inselberg (French Guiana), isolated vegetation clumps are mainly comprised of *Clusia minor* (Clusiaceae) and *Myrcia saxatilis* (Myrtaceae), two shrubs which characterize successive stages of primary plant succession in the locally called 'rock savanna' (Sarhou and Grimaldi, 1992). Places (2–5 m²) where dead stems of *C. minor* remain standing or have fallen ('micro-chablis') are often seen within shrub thickets (Sarhou, 1992). These zones of destruction, where intense termite activity occurs inside standing dead stems and branches, and where numerous sporocarps of wood-destroying fungi are found (Kounda-Kiki, 2007), offer evidence of destructive events of unknown origin and raise questions regarding dynamic processes generated by disturbance events such as pronounced dryness, fires, storms and fungal diseases (Finegan, 1984). Previous studies on the Nouragues inselberg (Kounda-Kiki et al., 2004, 2006; Vaçulik et al., 2004) showed that parallel changes occur in vegetation, humus profiles and soil animal communities throughout plant succession, but the existence of cyclic processes and the rate at which successional transition occurs are still under investigation.

We described humus profiles found in zones of destruction and compared them with humus profiles previously studied beneath pure *C. minor* thickets, as an early stage, and *C. minor* thickets enriched with *M. saxatilis* and several other Myrtaceae, as a late stage of plant succession (Kounda-Kiki et al., 2006). Based on visual inspec-

tion of the rock savanna, our hypothesis was that zones of destruction appear within pure, closed *C. minor* thickets, allowing more, new plant species to establish, in particular longer-lived Myrtaceae. If this hypothesis is true, then the composition of humus profiles in zones of destruction should fall between those under pure *Clusia* canopies and those under mixed *Clusia*–*Myrcia* canopies. We also investigated the predominant factors in the destruction of shrub thickets; factors that could be reflected in the composition of humus profiles as shown by Bernier and Ponge (1994) and Gillet and Ponge (2002) in temperate environments.

Materials and methods

Study site

The field work was carried out at the Nouragues inselberg (411 m above sea level), which is located in the Nouragues natural reservation (4°5'N and 52°42'W). The inselberg is composed of a tabular outcrop of Caribbean granite, of pinkish monzonitic-type, containing 27% potassium-feldspar (orthoclase), 37% plagioclase, 33% quartz as coarse-grained crystals and 2% accessory minerals such as pyroxene, corundum and apatite (Grimaldi and Riéra, 2001). The chemical composition of the entire outcrop (Sarhou and Grimaldi, 1992) indicated that the granite is highly siliceous (76.4% SiO₂) and rich in alkalis (4.6% K₂O, 4.2% Na₂O). The climate is tropical humid, and is characterized by a dry season from July to November and a wet season from December to June interrupted by a very short dry season in March. Mean annual precipitation reaches 3000–3250 mm. The daily temperature ranges between 18 and 55 °C and the daily air humidity between 20% and 100% (Sarhou and Grimaldi, 1992). The temperature of the bare rock surface can reach 75 °C in the dry season. Most of the surface of the granitic outcrop is covered by cyanobacteria (Sarhou et al., 1995). Different dynamic stages can be observed in the development of shrub thickets (Sarhou, 2001). The bromeliad *Pitcairnia geyskesii* is the most typical plant of the inselberg. *C. minor* (Clusiaceae) represents the shrub vegetation unit of the rock savanna, forming dense thickets, 2–8 m tall (Sarhou, 2001; Sarhou et al., 2003). *M. saxatilis* (Myrtaceae) is the second most important shrub species and is found within *C. minor* thickets together with other minor Myrtaceae. Zones of destruction are places with no living woody vegetation and only decaying stems of *C. minor*

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