



Clusia hilariana, A KEY SPECIES ON NUTRIENT CYCLING IN SAND DUNE VEGETATION THICKETS

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Abstract: Interspecific plant-plant interactions studies showed that *Clusia hilariana* plays a facilitation role in the scattered vegetation thickets of the Brazilian sandy coastal plain vegetation (Restinga). In the *Clusia* open formation in the Jurubatiba Restinga National Park there are thickets differing in the presence and senescence of *Clusia*: (1) healthy *Clusia* thickets (HCT); (2) senescent *Clusia* thickets (SCT); and also (3) thickets without *Clusia* (TWC). The aim of this long term study was to assess soil chemistry, litterfall mass and nutrient input and its leaf-litter decomposition in *Clusia* thickets, testing the hypotheses that: (1) the presence of *Clusia* increases soil nutrient concentrations in the thickets; (2) litterfall mass and nutrient input are dependent on the senescence stage of *Clusia*, being higher in HCT than in SCT; (3) decomposition and nutrient release of *Clusia* leaves are faster in HCT than in SCT, evaluating if *C. hilariana* promotes an improvement in nutrient cycling according to its presence and senescence in the thickets and reinforcing the role of *Clusia* as a nurse plant. Collection of nutrients in soils, litterfall and *Clusia* leaf decomposition rates were measured between 2001 and 2008. The HCTs presented higher annual litterfall mass and nutrient input than the SCTs, *Clusia* leaf-fall contributed the bulk of the total litterfall (70 % HCT, 34 % SCT). Nitrogen, as all other nutrient inputs from *Clusia* leaf-litter, was higher in HCT, although *Clusia* leaves had low N concentrations and a higher C/N ratio. *Clusia*-leaf decomposition was faster in HCT than in SCT during the first year of the experiment. The slow decomposition and nutrient release from *Clusia* leaf-litter, may be an important mechanism of nutrient conservation. We concluded that *C. hilariana* acts as a key species, and as a nurse plant, in relation to nutritional dynamics, organic matter, nutrient input, and decomposition via its litter, which decreased according to its senescence.

Keywords: decomposition; litterfall; nurse plant; restinga; soil.

INTRODUCTION

Facilitation through nurse plants is a common process in arid ecosystems (Scarano *et al.* 2004,

Navarro-Cano *et al.* 2019). Factors such as salinity, low nutrient and water availability create a gradient of stressful conditions in coastal sandy dune vegetation, triggering species facilitation

mechanisms (Dalotto *et al.* 2018). This facilitation process include mechanisms such as changes in microclimate through decreasing air and soil temperature and increase in nutrient availability as a consequence of nurse species' role (Vetaas 1992, Franco *et al.* 1996, Dalotto *et al.* 2018), promoting a more favorable environment for different plant species and their occurrence (Franco & Nobel 1989, Drezner 2003).

It has been noticed that species with large crowns and dense canopies are good facilitators (Arantes *et al.* 2014), as they reduce incident radiation and soil temperature, as well as promote an increase in nutrient availability through litterfall (Brooker *et al.* 2007). A recent experimental study in an area of semi-arid mine tailings in Spain, demonstrated the nurse plants role as co-drivers of an essential ecosystem function, influencing nutrient cycling processes (Navarro-Cano *et al.* 2019). Trees canopies have a great influence on nutrient cycling in forests related to their role as the main source of leaf litter (Prescott 2002). It is known that plant species create feedbacks to the patterns of nutrient cycling in natural ecosystems (Haghverdi & Koock 2019) changing nutrient concentrations and availability in distinct compartments. Species effects have been found to be more important than abiotic factors in controlling ecosystem fertility (Hobbie 1992, 2015) and nutrient cycling in tropical forests (Villega & Proctor 1999, Villega *et al.* 2006). The leaves of each species may have distinct decomposition rates and nutrient release depending on their quality and the environment may be determinant for its functioning and dominance (Villega & Proctor 2002).

Litter cover may alter soil physical and chemical properties, promoting lower soil temperature and evapotranspiration and higher nutrient availability in understory (Vetaas 1992). Some experiments have shown that changes in species composition are associated with an increase in nitrogen mineralization during succession (for example, Berendse *et al.* 1998). Nutrient cycling and allocation patterns may also be affected by the successional stage of the vegetation (Ewel 1976, Brown 1982, Vitousek 2004, Camara *et al.* 2018). As emphasized in previous studies (e.g. Congdon & Herbohn 1993, Vitousek 2004, Villega *et al.* 2006), an understanding of nutrient cycling processes is fundamental to the management of natural and

disturbed vegetation growing on tropical soils of low fertility. Several studies have focused on nutrient cycling and dynamics in the Atlantic forest in the last decades (e.g. Villega *et al.* 1998, Kindel *et al.* 1999, Villega *et al.* 2006, 2012, Silva & Villega 2015, Martinelli *et al.* 2017, Camara *et al.* 2018). Some of those have been also done out in restinga (e.g. Hay & Lacerda 1984, Henriques *et al.* 1992, Ramos & Pellens 1993, Brietz *et al.* 2005, Pires *et al.* 2006, Brito *et al.* 2018).

Interspecific plant-plant interactions studies at Jurubatiba Restinga National Park have shown that *C. hilariana* has a major facilitation role and is also considered to be a nurse plant in succession in this vegetation community (Zaluar & Scarano 2000, Scarano *et al.* 2004, Dias & Scarano 2007, Luttge 2007, Correia *et al.* 2010). The Brazilian sandy coastal plain vegetation (restinga) is composed of different formations (Araújo & Pereira 2009). One of these is called open *Clusia* scrub formation, composed of scattered vegetation thickets where the plant species *Clusia hilariana* (Clusiaceae) occupy a key position (Zaluar & Scarano 2000, Araújo & Pereira 2009). Seedlings of the most important species of this vegetation formation were under *Clusia* thickets (Pimentel *et al.* 2007). The open *Clusia* formation has one of the highest areas in this restinga with the preeminent species richness and density of Bromeliaceae (Cogliatti-Carvalho *et al.* 2001). According to these authors, it may be related to an increase in plant coverage and consequently its environment favorability inside to the thickets (Zaluar 2000).

In a review of crassulacean acid metabolism (CAM) species Luttge (2010) highlighted that CAM plants can be dominant in distinct ecosystems, with essential contributions to their functioning. The CAM plant *C. hilariana* has traits that distinguish it from other species in the Restinga and mainly from those that also occur in the Atlantic Rainforest (Rosado & De Mattos 2010). Even so, there are still few studies that have measured the contribution of CAM plants, such as *C. hilariana*, to the total budgets and turnover of energy and matter, carbon, water and mineral nutrients (Luttge 2010). *Clusia hilariana* was shown to have a significant contribution to biomass stock in the nutrient-poor Restinga of Jurubatiba (Dias *et al.* 2006) and to the organic matter turnover (Scarano *et al.* 2004, Brito *et al.* 2018), with a conservative

strategy of carbon acquisition (Dias & Scarano 2007). Although the clumped distribution pattern of plants at the restinga has called attention since the beginning of the century (Zaluar & Scarano 2000, Luttge 2007, Araújo & Pereira 2009), not much is known about its successional process (Dias & Scarano 2007, Correia *et al.* 2010), particularly in relation to nutrient dynamics and limitation (Silva 1999, Scarano *et al.* 2004, Dias *et al.* 2006, Brito *et al.* 2018).

In the open *Clusia* formation landscape of Jurubatiba Restinga National Park, there are thickets with different senescent stages of *C. hilariana* (Scarano *et al.* 2004, Dias & Scarano 2007). Some are composed of mature adults with a closed canopy, healthy *Clusia* shrubs with a dense canopy, called here as Healthy *Clusia* Thickets (HCT) and other thickets composed by senescent *C. hilariana* individuals with an open canopy called Senescent *Clusia* Thickets (SCT) (Scarano *et al.* 2004, Dias & Scarano 2007). This mosaic of situations of *Clusia* at distinct successional stages distributed in the same landscape, has stimulated crucial questions on ecological processes which may drive restinga communities (eg. Scarano *et al.* 2004, Dias & Scarano 2007). Therefore, in order to achieve a comprehensive understanding of the role of *C. hilariana* species as a key plant in the context of nutrient cycling, the aim of this long term study was to assess soil chemistry, litterfall mass, nutrient input and its leaf-litter decomposition in *C. hilariana* thickets in the sandy coastal plain vegetation of the Jurubatiba Restinga National Park (PELD Site 5), testing the following hypothesis: (1) the presence of *Clusia* increases soil nutrient concentration, in a way that HCT and SCT soils are higher in nutrients than in thickets without *Clusia* (TWC); (2) litterfall mass and nutrient input are dependent of the senescence stages of *C. hilariana*, being higher in HCT than in SCT, mainly as a consequence of *C. hilariana* leaves contribution; (3) decomposition and nutrient release of *C. hilariana* leaves are faster in HCT than in SCT, because of the favorability of its environmental conditions below a closer canopy. Thus, if *C. hilariana* promotes an improvement in nutrient cycling according to its presence and senescence in these thickets the question relating this pattern to the role of *C. hilariana* as a nurse plant may be answered.

MATERIAL AND METHODS

Study area

The Jurubatiba Restinga National Park (22°00' - 22°23'S; 41°15' - 41°45'W) in southeast Brazil (Figure 1) is composed of ten different vegetation formations. One of the most representative formation in this Park is the open *Clusia* scrub formation covering up to 32 % of its area. This formation is characterized by thickets spread over a white sand soil and the species *Clusia hilariana* Schlttdl. is the most representative, dominating most thickets (Araújo *et al.* 1998, Araújo & Pereira 2009). Thickets dominated by other species are less frequent and interspersed in the landscape. These patches include C3 species as *Protium icicariba*, *Ocotea notata* and *Tapirira guianensis*. Distances between patches vary from zero (connected patches) to about 20 m (Dias *et al.* 2005). The climate type in the region is Aw (Tropical with dry winters) according to Köppen classification. The mean annual rainfall in the region is 1,100 to 1,250 mm, with a lower precipitation from June to August. The mean annual temperature varies between 21.3 and 22.4°C (Alvares *et al.* 2013). More detailed descriptions about the study site and *C. hilariana* are found in Araújo *et al.* (1998), Dias *et al.* (2005, 2006), Scarano *et al.* (2005), Dias & Scarano (2007), Pimentel *et al.* (2007) and Correia *et al.* (2010). Three types of thickets were selected for the present study in the open *Clusia* thicket formation in the Jurubatiba Restinga National Park: adult Healthy *Clusia* Thickets (HCT, N = 6), with a closed *Clusia* canopy; adult Senescent *Clusia* Thickets (SCT, N = 6), with a partially open *Clusia* canopy; and Thickets Without *Clusia* (TWC, N = 6), dominated by *Protium icicariba*. These thickets were selected in 2001 by the PELD –site 5 group, and other studies on floristic composition, vegetation structure, ecophysiology, ecology etc. have been carried out at this local (eg. Mantuano 2003, Ramos 2003, Scarano *et al.* 2004, Pimentel *et al.* 2007, Correia *et al.* 2010). Other authors have denominated these thickets differently, using mature *Clusia* patches, senescent *Clusia* patches and plant patches without *Clusia* dominance (Dias & Scarano 2007). In the present study we decided to use the term “healthy” for HCT, as the senescent individuals in the SCT are older, closer to dying, while the mature adult *C. hilariana* individuals in

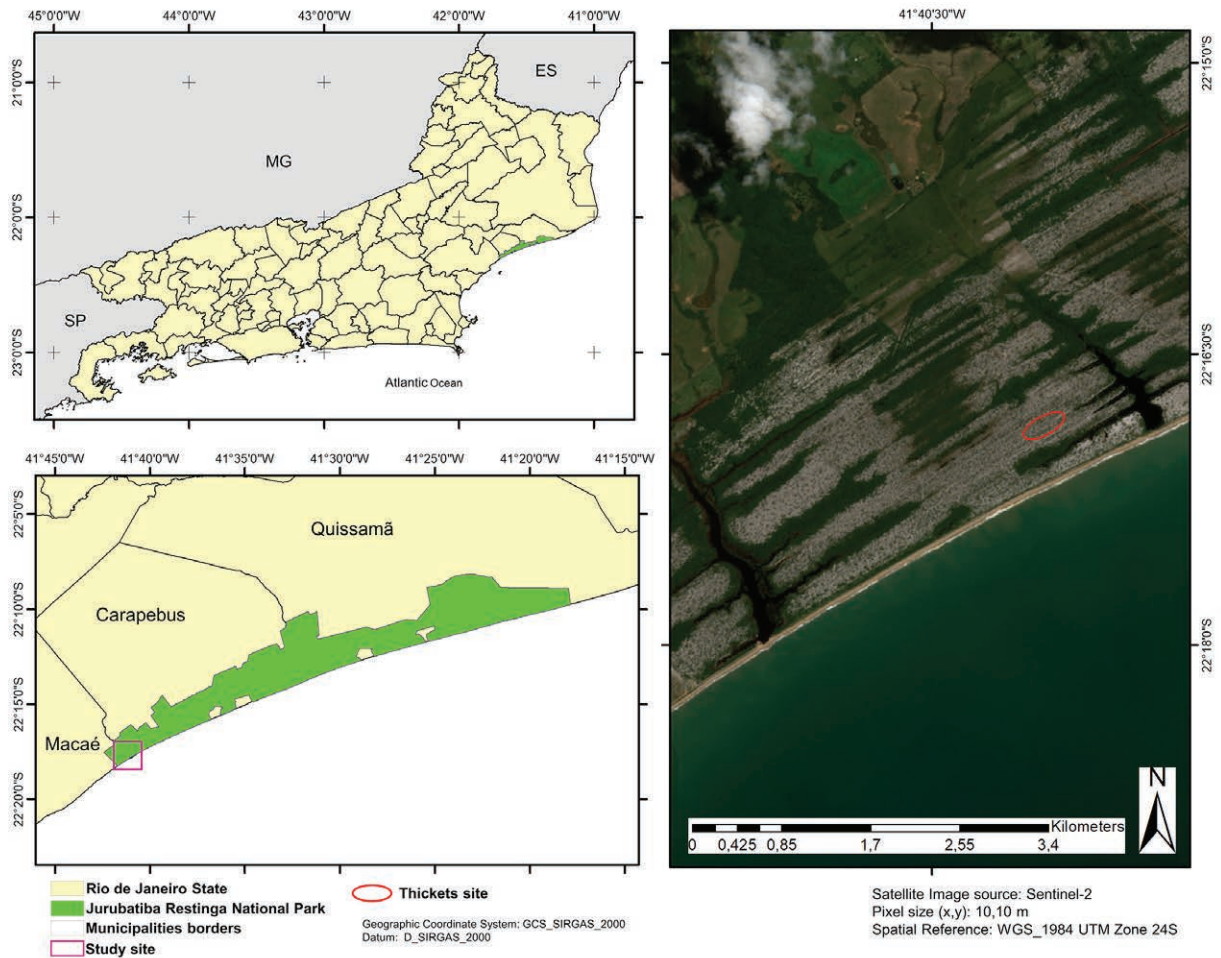


Figure 1. Location of the Jurubatiba Restinga National Park (*Parque Nacional da Restinga de Jurubatiba*, Carapebus, Rio de Janeiro State, Brazil). Red area represents the site of the thickets studied (HCT, SCT, TWC).

HCT are healthy, with no signs of senescence or diseases (Scarano *et al.* 2004).

The selected thickets are similar in size: HCT = 35-124 m²; SCT = 44-112 m²; TWC = 32-109 m². Although *Clusia* thickets have similar heights (HCT = 3.8 m; SCT = 4.0 m) and basal areas (HCT = 0.33 m²; SCT = 0.35 m²), tree density is lower in the HCT understory (Ramos 2003). HCT also has a higher canopy area (HCT = 74 m; SCT = 69 m) and leaf area index (HCT = 0.00609; SCT = 0.00376; Mantuano 2003). Species floristic composition and structure are similar between the two thicket types (Mantuano 2003, Pimentel *et al.* 2007, Correia *et al.* 2010), and the most important species under these *Clusia* thickets are *Erythroxylum subsessile*, *Myrcia lundiana* and *Mirsyne parvifolia* (Mantuano 2003). During the first year of the decomposition experiment (from November 2004 to November 2005), air temperature and humidity were measured

in the sampling dates using Thermohygrometer (445702/EXTECH) under the thickets (Bonadiman 2007). The temperature of soil surface (3 cm depth) was measured using mercury thermometer and the humidity of the first 10 cm soil surface gravimetrically (Allen 1989, Bonadiman 2007). Air humidity was similar between thickets (56 %), but soil humidity tended to be higher in HCT (5.7 %) than in SCT (4.7 %), while temperatures (T) were lower in HCT (Air T = 36.9 °C; Soil T = 28.2 °C) than in SCT (Air T = 37.8 °C; Soil T = 30.6 °C).

Experimental design

One bulk surface soil sample (0-10 cm) composed of three sub-samples was collected in each thicket (N = 18) during the dry season (September/2001). Samples were dried (40 °C) and sieved (< 2.0 mm). Litterfall was sampled in three 30 cm x 40 cm (0.12 m²) traps, 20 cm above the soil surface below each

Clusia thicket, HCT and SCT, but not in TWC. Litterfall was collected at 15-d intervals from 29 September 2001 to 02 October 2002 and monthly in the following consecutive years until October 2007. It was dried at 80 °C/24 h and sorted into fractions according to Proctor (1983), Villela & Proctor (1999) and Villela *et. al.* (2006): *Clusia* leaves; other leaves; wood; flowers & fruits; and trash fractions, considering both *Clusia* and other species together. After, each fraction was dried again and weighed.

For the decomposition experiment approximately 5 g of air dried *C. hilariana* leaves were placed in 20 cm x 24 cm nylon bags (1.5 mm mesh, with six 10-15 mm holes; Villela & Proctor 2002). Only freshly fallen senescent leaves showing negligible signs of decomposition were used. Three groups of 16 litter bags each, composed of *Clusia* leaves collected in the specific thicket type and were placed randomly on the soil surface in each HCT and SCT thicket on 24 November 2004. Three litter bags were collected from each thicket at the following days after the experiment began: 15, 30, 59, 90, 126, 183, 254, 305, 373, 427, 515, 610, 701, 796, 960, 1059 days. The leaves were retrieved from the bags, cleaned, oven dried (80 °C) and weighed (Villela & Proctor 2002).

Chemical analysis

Soil 2-4 mg sub-samples from each soil sample were sieved to $\leq 63 \mu\text{m}$ for C and N analysis. Total C and N were determined using a CHN/S auto-analyser. Sub-samples of soil (10 g) were leached by ten successive additions of 10 ml 1M ammonium acetate solution adjusted to soil pH with acetic acid for ion determination using an ICP – AES (Varian Liberty Series II) (Allen 1989). Extractable ($[\text{Al}^{3+}] + [\text{H}^+]$) was determined in 10 g of soil leached with KCl 1 M (EMBRAPA 1997). Cation exchange capacity (CEC) was estimated by the sum of cations ($\text{Al}^{3+} + \text{H}^+$), Ca^{2+} , Mg^{2+} , K^+ e Na^+ (EMBRAPA 1997).

The litterfall samples of the first year (29 September 2001 to 02 October 2008) were bulked for each two consecutive month period from the three traps in each thicket for all fractions for the chemical analyses. Three litterbags were bulked per each thicket in each sampling date for chemical analysis of the nutrient release in the decomposition experiments of the leaf samples in the litterbags from the first year of the experiment (time zero, 15, 30, 59, 90, 126, 183, 254, 305, 373

days). The litter samples were ground in an electric mill for chemical analysis. Sub-samples were homogenized and sieved to $\leq 63 \mu\text{m}$ for total C and N determination using a CHN/S auto-analyser. For cations, sub-samples (*ca* 0.20 g dry weight) of each ground sample were digested in 4.4 ml of concentrated sulphuric acid (350 ml), 100 volume hydrogen peroxide (420 ml), selenium (0.42 g) and lithium sulphate (14 g, Allen 1989). Calcium, K, Mg and Na were determined using an ICP – AES (Varian Liberty Series II). All chemical analyses were carried out in the Environmental Sciences Laboratory (LCA) at UENF University, Brazil.

Data analysis

Two regression equation models were used to fit the curve of the rate of mass loss in the litter bags to estimate the decomposition constant (k ; Olson 1963): linear ($X = C_1 - k_1t$); and single exponential ($X = e^{-k_2t}$); where X is the proportion of initial mass (X_0) remaining at time t , k 's are decomposition constants, and C 's are other constants. The single exponential showed the best fit (R^2 , HCT = 0.979; SCT = 0.969) and was used to estimate k . Half-life of leaves was estimated based on k of the leaves (when 50 % mass dry weight of leaves are lost), where:

$$-\ln(0.5)/k = 0.693/k, \text{ then, } t_{0.5} = 0.693/k \text{ (Olson 1963)}$$

Linear regressions between *C. hilariana* leaf litter dry weight in the litterbags and each of their nutrient concentrations were made to determine if the concentration was a function of the percent original dry mass (Villela & Proctor 2002).

Between-area comparisons of the soil properties, annual litterfall and decomposition mass and concentrations and quantities for each bulked sample were tested using one-way analysis of variance (ANOVA) (Zar 1984). To test differences in litterfall and decomposition mass and nutrient concentration and quantities between areas with time, an ANOVA with repeated measurement design was used. For this analysis, time was considered the within-subject factor, and area and plot, the between-subject factor. Multiple comparisons of the forest means were made using a Tukey test considering $p < 0.05$ as significant (Zar 1984). The analyzes cited were performed in the R environment (v. 3.6.1, R Core Team 2019).

RESULTS

Surface soil chemistry in the thickets

Only Na concentration was significantly different among the soil thickets ($p < 0.05$), being 23% lower in HCT and TWC than in SCT (Table 1). The concentrations of Ca, Mg, K, C/N ratio and CEC were also lower, but without a significant difference in HCT soils compared to SCT (Table 1).

Litterfall production and nutrient input

Considering the mean of the seven-year period, the total litterfall was significantly higher in HCT than in the SCT ($F = 36.24$, $p < 0.001$; Table 2), as it was for each year separately (Supplementary Table S1). This difference was mainly a response

of *Clusia* leaf-litter mass, which was almost four times greater in HCT than in SCT (Table 2). Only other leaves and wood fractions were 39% and 28 %, respectively lower in HCT than in SCT. Wood was the only fraction that did not differ significantly between tickets (Table 2).

The *Clusia* leaf fraction was the bulk of the litterfall, mainly in HCT where it accounted for 70% of the total litterfall, being significantly higher than other leaves (11%), wood (11%), flowers & fruits (4%) and trash (4%) (Table 2). In the SCT, *Clusia* leaves represented half of the annual leaf-litterfall production (34%), and was still significantly higher than other leaves, that corresponded the other half portion of the leaf-litterfall (30%), followed by wood (26%), flowers & fruits (4%) and trash (6%).

The differences between thickets were also

Table 1. Means and standard deviations of soil pH, organic matter (OM), C, N (%), C/N ratio, exchangeable cations (Mequiv/kg) and cation exchange capacity (CEC) in healthy *Clusia* thickets (HCT, N = 6), senescent *Clusia* thickets (SCT, N = 6) and thickets without *Clusia* (TWC, N = 6) in the Jurubatiba Restinga National Park, RJ. Values within a column followed by different letters are significantly different.

| Thicket | pH | % | | | C/N | (Mequiv/kg) | | | | | CEC |
|---------|------|----|-----------|-------------|-----|-------------|-----------|-------------|--------------------------|----------------------------------|------------|
| | | OM | C | N | | Ca | Mg | K | Na | H ⁺ +Al ³⁺ | |
| HCT | 4.46 | 4 | 3.0 ± 1.2 | 0.21 ± 0.11 | 15 | 4.8 ± 1.4 | 4.4 ± 1.9 | 0.49 ± 0.13 | 0.85 ± 0.21 ^a | 2.2 ± 0.75 | 12.7 ± 3.8 |
| | | | SCT | 4.49 | | 6 | 3.7 ± 1.4 | 0.18 ± 0.06 | 21 | 6.6 ± 1.9 | 5.2 ± 1.7 |
| TWC | 4.13 | 6 | 3.7 ± 0.9 | 0.19 ± 0.05 | 20 | 4.7 ± 2.5 | 4.2 ± 1.8 | 0.58 ± 0.11 | 0.80 ± 0.14 ^a | 2.4 ± 0.82 | 12.7 ± 3.8 |

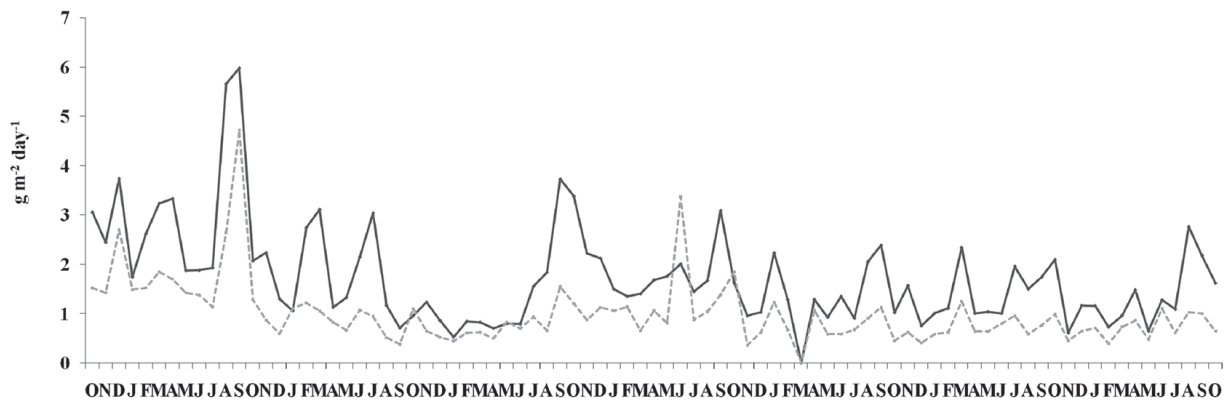
Table 2. Litterfall ($t\ ha^{-1}yr^{-1}$) in the Jurubatiba Restinga National Park, RJ, Brazil. Values for means and standard deviations for three traps in each thicket type: healthy *Clusia* thickets (HCT, N = 6); senescent *Clusia* thickets (SCT, N = 6). The uppercase letters within the same row (**A** and **B**), indicate significant differences (One-Way-ANOVA- $p < 0.05$) between the thicket types, for each fraction. The lowercase letters within the same column (**a, b, c, d, e, f, g**) indicate significant differences among fractions within each thicket type (ANOVA $p < 0.05$).

| | Litterfall ($t\ ha^{-1}\ year^{-1}$) | |
|----------------------|--|-----------------------------|
| | HCT | SCT |
| <i>Clusia</i> leaves | 3.9 ± 1.3 ^{Aa} | 1.1 ± 0.8 ^{Ba} |
| Other leaves | 0.59 ± 0.27 ^{Abc} | 0.97 ± 0.73 ^{Bbc} |
| Wood | 0.59 ± 0.36 ^{be} | 0.82 ± 0.53 ^{bdg} |
| Flower/fruit | 0.25 ± 0.18 ^{Ab} | 0.14 ± 0.13 ^{Bbeh} |
| Trash | 0.26 ± 0.11 ^{Abdf} | 0.18 ± 0.10 ^{Bbfi} |
| Total litterfall | 5.6 ± 1.3 ^A | 3.2 ± 1.1 ^{Bb} |

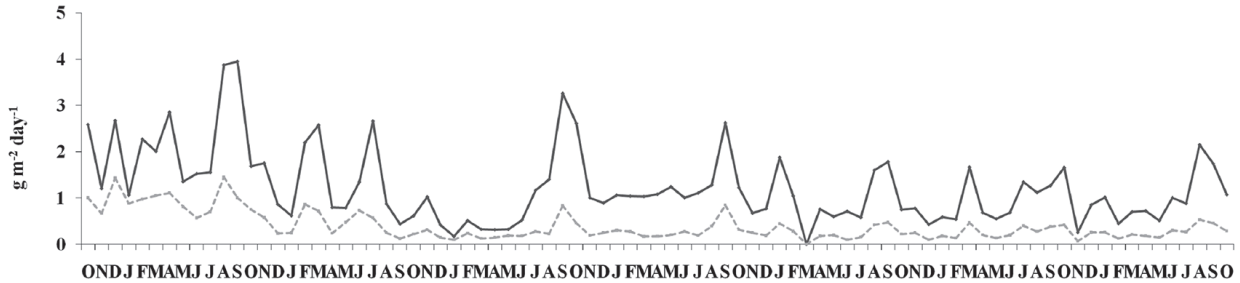
significant considering the litterfall along the seven years period (Supplementary Table S1; Repeated ANOVA $p < 0.05$), that was always higher in HCT considering the total and *Clusia* leaf litterfall (Figure 2). Seasonal variation of litterfall was evident in both thicket types (Figure 2), with peaks in the dry

season (August to October) and occasionally in the rainy season (January to March). The annual total litterfall reflected mainly leaf fractions, especially *Clusia* leaf-fall in the HCT (Figure 2). Other leaves, wood and trash also showed a higher litterfall in the dry season in both thicket types.

(A)



(B)



(C)

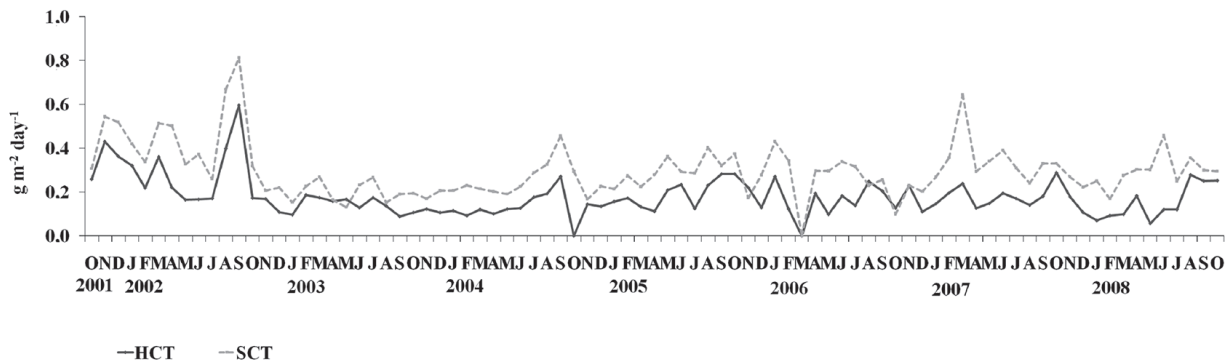


Figure 2. Seasonal variation of total litterfall (A), *Clusia* leaves (B) and other leaves (C) in the litterfall ($\text{g m}^{-2} \text{day}^{-1}$) in healthy *Clusia* thickets (HCT, $N = 6$) and senescent *Clusia* thickets (SCT, $N = 6$) from 14th October 2001 to 30th October 2008, in the Jurubatiba Restinga National Park, RJ, Brazil. Values indicate means among 18 traps (0.12 m^{-2}) in each of the 6 thickets type per month.

The concentrations of the litterfall nutrients analyzed were in general not significantly different between thickets (Table 3). For the total annual litterfall, only Mg concentration was significantly 21 % higher in HCT than in SCT and Na was 6 % lower in HCT (Table 3). *Clusia* leaf-litter also showed the same differences. Other leaves presented higher concentrations of Mg and K in HCT than in SCT. Calcium and Na concentrations were higher and N and K lower in *Clusia* leaves than in other leaves (Table 3) in both thicket types. Calcium concentrations in *Clusia* leaves were similar to that in wood fraction. Sodium concentration in *Clusia* leaves was higher than in any other fraction and C/N ratio was higher than in other leaves (Table 3).

Quantities of nutrients in the total annual litterfall were significantly higher in HCT than in SCT (Table 4), except for Na. This pattern was observed for all nutrients analysed in the *Clusia* leaf litterfall (Table 4).

***Clusia* leaf-litter decomposition and nutrient release**

The decomposition of *Clusia* leaves was faster in the HCT than in the SCT during the first year of the experiment. The mass loss was significantly higher in the HCT, where 31 % of *Clusia* leaf-litter decomposed until 373 days of the experiment, compared to 26 % decomposed below the SCT

canopy (Figure 3). However, considering the whole experiment (1059 days) the mass loss was not significantly different between thickets, even though there was a trend of a higher mass loss in the HCT at the end of the three years of the experiment when 58 % of *Clusia* leaf-litter was decomposed below the HCT canopy compared to 53 % in the SCT (Figure 3). Mass loss of *Clusia* after 120 days from the beginning of the experiment was about 20% in both thickets, while from 120 to 373 days, it was only 10 %.

In the first year of the experiment (considered up to 373 sampling days), the decomposition rate was higher in the HCT ($k = 0.29$), where half-life estimated for *Clusia* leaves was 866 days, while in the SCT ($k = 0.22$) it was estimated to be 1155 days. Although considering the whole period of the experiment (1059 days) the decomposition rate was the same between the thickets ($k = 0.29$).

In general, nutrient concentrations in decomposing *Clusia* leaves differed significantly between the two thicket types, where Ca and Mg concentrations were higher in the HCT and K and Na in the SCT (Figure 4). Only K had a faster release in the HCT than in the SCT during the decomposition process (Figure 5), showing a net release in the HCT. Na also released rapidly in both *Clusia* thicket types studied (Figure 5).

Table 3. Mean concentration (mg g^{-1} oven dry weight) of nutrients and C/N ratio (SD) in litterfall collected during one year (2001 to 2002) from one bulked sample per thicket (HCT, SCT) in the Jurubatiba Restinga National Park, RJ. Values within the same column followed by different letters are significantly different between thickets (One-Way-ANOVA- $p < 0.05$), within each fraction. *For C and N, trash was composed of the fractions: wood, flower/fruit and trash.

| Fractions | Thickets | Nutrient concentration in litterfall (mg g^{-1}) | | | | | | |
|------------------|----------|---|------------------------|------------------------|------------------------|---------|------------|-----|
| | | Ca | Mg | K | Na | C | N | C/N |
| Clusia leaves | HCT | 8.3 ± 0.7 | 2.9 ± 0.3 ^a | 0.9 ± 0.2 | 4.4 ± 0.4 ^a | 479 ± 5 | 5.9 ± 0.6 | 81 |
| | SCT | 7.7 ± 0.4 | 2.3 ± 0.3 ^b | 1.0 ± 0.1 | 6.2 ± 0.5 ^b | 481 ± 4 | 6.0 ± 0.3 | 80 |
| Other leaves | HCT | 6.2 ± 0.3 | 2.6 ± 0.4 ^a | 2.4 ± 0.5 ^a | 3.3 ± 0.8 | 483 ± 8 | 9.5 ± 0.4 | 51 |
| | SCT | 5.7 ± 0.5 | 2.1 ± 0.2 ^b | 1.7 ± 0.3 ^b | 3.6 ± 0.9 | 488 ± 6 | 8.9 ± 0.8 | 55 |
| Wood | HCT | 8.0 ± 2.7 | 1.7 ± 0.3 | 0.7 ± 0.2 | 0.9 ± 0.3 | — | — | — |
| | SCT | 7.2 ± 1.0 | 1.3 ± 0.2 | 0.7 ± 0.3 | 1.3 ± 0.5 | — | — | — |
| *Trash | HCT | 5.4 ± 1.0 | 2.2 ± 0.4 | 4.4 ± 0.9 | 3.4 ± 1.2 | 470 ± 8 | 10.4 ± 1.4 | 45 |
| | SCT | 5.7 ± 0.6 | 1.9 ± 0.2 | 4.5 ± 0.7 | 3.2 ± 0.7 | 470 ± 5 | 10.1 ± 1.3 | 46 |
| Total Litterfall | HCT | 6.9 ± 0.9 | 2.3 ± 0.2 ^a | 2.1 ± 0.2 | 3.0 ± 0.5 ^a | 477 ± 3 | 8.6 ± 0.6 | 56 |
| | SCT | 6.6 ± 0.3 | 1.9 ± 0.2 ^b | 2.0 ± 0.2 | 3.6 ± 0.4 ^b | 480 ± 2 | 8.4 ± 0.3 | 57 |

Table 4. Nutrient input from litterfall ($\text{kg ha}^{-1} \text{ year}^{-1}$). The values indicate average of one sample composed of sub-samples per thicket (HCT, $n = 6$; SCT, $n = 6$) in the Jurubatiba Restinga, Carapebus, RJ. Values within the same column followed by different letters are significantly different (One-Way-ANOVA- $p < 0.05$) between thickets for each fraction. * The fraction trash for C, N e C/N was composed of the fractions: wood, flower & fruit and trash.

| Fractions | Thickets | Nutrient input from litterfall ($\text{kg ha}^{-1} \text{ year}^{-1}$) | | | | | |
|------------------|----------|--|------------------|------------------|------------------|-----------------|------------------|
| | | C | N | Ca | Mg | K | Na |
| Clusia leaves | HCT | 1.783 ± 476^a | 21.5 ± 6.5^a | 31.0 ± 4.3^a | 11.0 ± 2.2^a | 3.9 ± 1.4^a | 16.4 ± 3.7^a |
| | SCT | 969 ± 410^b | 12.1 ± 4.9^b | 12.9 ± 3.9^b | 4.2 ± 1.2^b | 1.9 ± 0.5^b | 10.9 ± 3.0^b |
| Other leaves | HCT | 258 ± 66 | 5.2 ± 1.2 | 3.1 ± 0.8 | 1.3 ± 0.2 | 1.2 ± 0.7 | 1.5 ± 0.5 |
| | SCT | 388 ± 231 | 6.5 ± 3.6 | 3.6 ± 1.8 | 1.7 ± 1.2 | 1.5 ± 1.0 | 2.8 ± 2.2 |
| Wood | HCT | — | — | 4.0 ± 1.9 | 0.9 ± 0.6 | 0.3 ± 0.1 | 0.4 ± 0.2 |
| | SCT | — | — | 4.9 ± 3.4 | 0.9 ± 0.5 | 0.3 ± 0.2 | 0.5 ± 0.4 |
| *Trash | HCT | 489 ± 156^a | 9.7 ± 3.9 | 2.3 ± 1.0^a | 0.9 ± 0.5^a | 1.9 ± 1.0 | 1.4 ± 0.7^a |
| | SCT | 450 ± 232^b | 9.7 ± 4.8 | 1.2 ± 0.5^b | 0.4 ± 0.2^b | 1.0 ± 0.6 | 0.7 ± 0.3^b |
| Total Litterfall | HCT | 2.531 ± 432^a | 36.5 ± 6.0^a | 40.5 ± 3.7^a | 14.2 ± 2.0^a | 7.4 ± 1.0^a | 19.7 ± 4.2 |
| | SCT | 1.808 ± 536^b | 28.4 ± 7.9^b | 22.6 ± 5.9^b | 7.3 ± 1.7^b | 4.7 ± 1.6^b | 15.0 ± 2.7 |

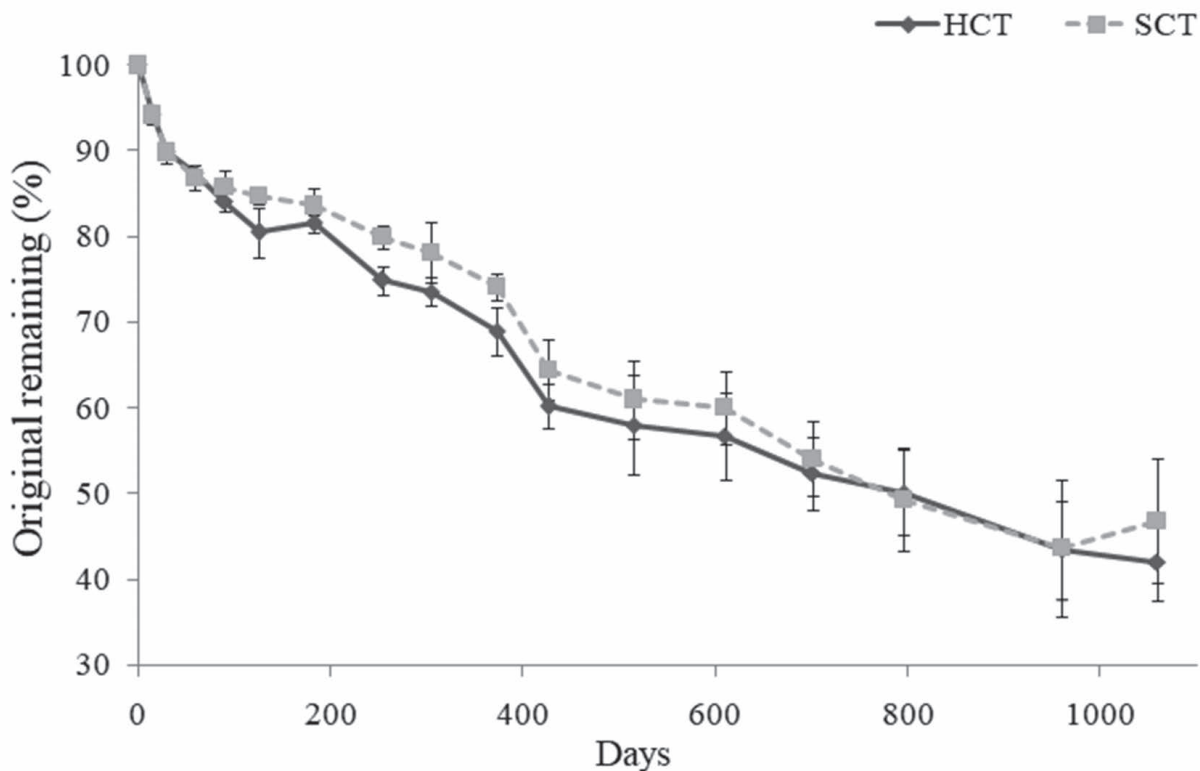


Figure 3. Percentage (Mean \pm SD, $N = 6$) original dry mass remaining with time (1059 days) for *Clusia hilariana* leaves in litterbags in Healthy *Clusia* thickets (\blacklozenge HCT) and Senescent *Clusia* Thickets (\blacksquare SCT) in the Jurubatiba Restinga National Park, RJ, Brazil.

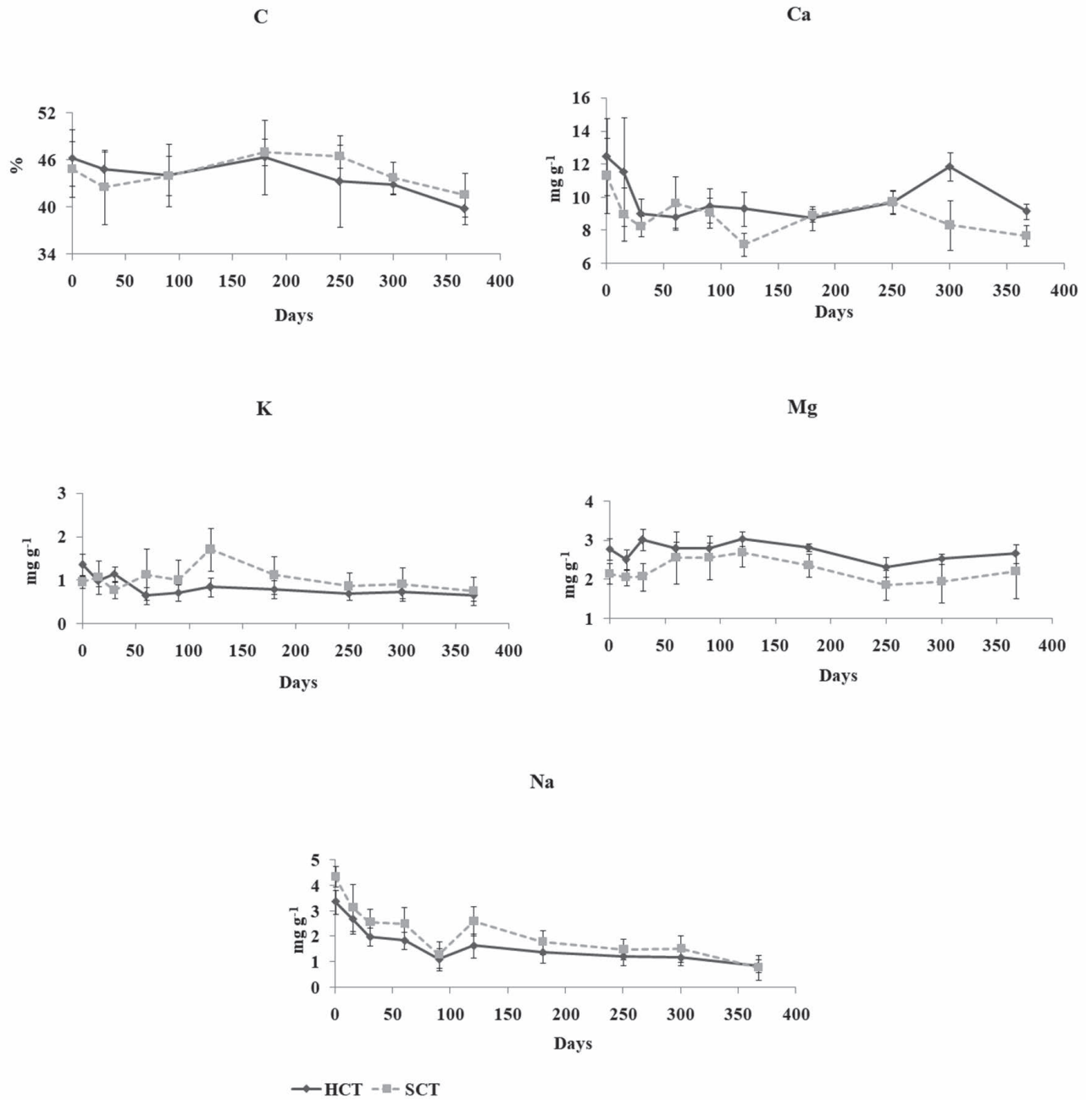


Figure 4. Concentrations (Mean \pm SD, N = 6) of C (%), Ca, K, Mg and Na (mg g⁻¹) in decomposing *Clusia hilariana* leaves over time (367 days) in healthy *Clusia* thickets (◆HCT) and senescent *Clusia* thickets (■SCT) in the Jurubatiba Restinga National Park, RJ, Brazil.

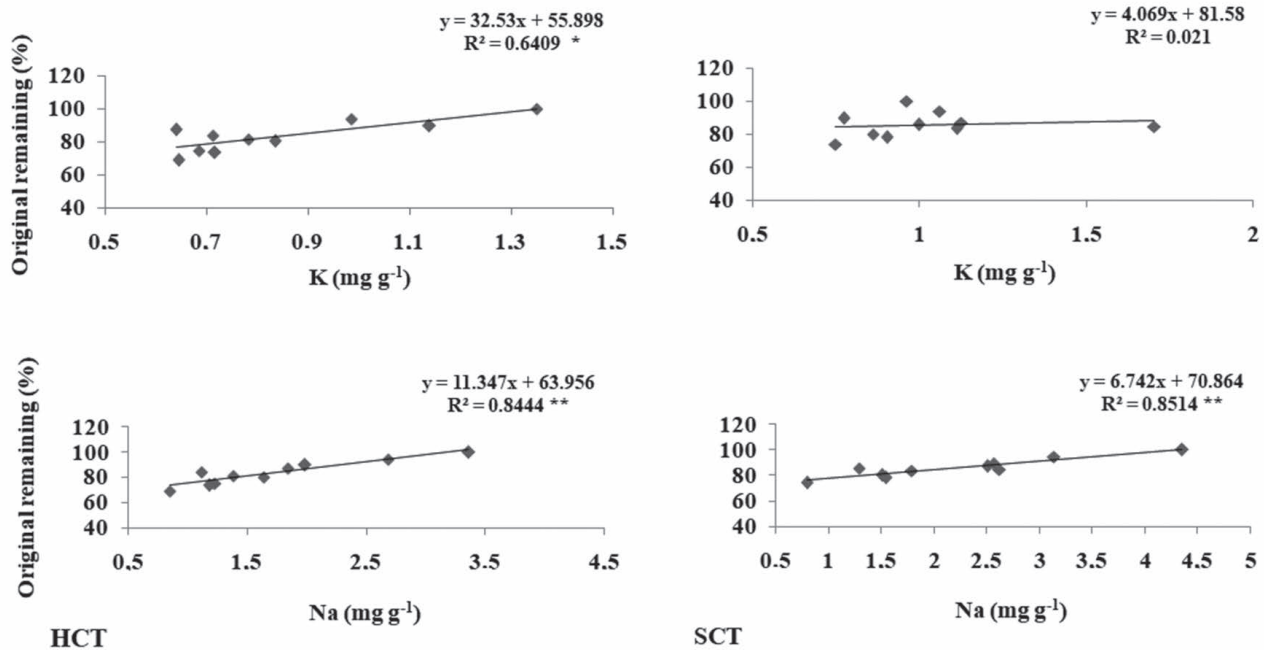


Figure 5. Potassium (K) and sodium (Na) concentrations (mg g^{-1}) as a function of the original percentage of dry mass of *Clusia hilariana* leaves in healthy *Clusia* thickets (HCT) and senescent *Clusia* thickets (SCT) in the Jurubatiba Restinga National Park, RJ, Brazil. NS = not significant, * = $P < 0.05$, ** = $P < 0.01$.

DISCUSSION

The higher litterfall in the HCT than in the SCT was a consequence of *Clusia* leaf-litter in these thickets, which was influenced by its senescent stage, corroborating the hypotheses 2. *Clusia hilariana* was the dominant species in the thickets, and its leaves represented up to 70 % of the total litterfall in the thicket during the present study. The higher canopy area and leaf area index of *Clusia* in the HCT (Mantuano 2003), could lead to a higher total leaf mass in these thickets. Also, tree density of other species was lower in the HCT understory (Ramos 2003) and senescent *Clusia* thickets had a distinct species distribution (Mantuano 2003, Correia *et al.* 2010), that explains other leaf fractions being 50 % lower in the HCT than in the SCT. Other thickets with *Clusia* in the Jurubatiba Restinga presented similar litterfall production ($4.7 \text{ t ha}^{-1} \text{ yr}^{-1}$) compared to thickets without *Clusia* ($4.0 \text{ t ha}^{-1} \text{ yr}^{-1}$) in studies carried out from 2012 to 2014 by Brito *et al.* (2018), with 81 % and 65 % of leaves in the total litterfall, respectively, but the contribution of *C. hilariana* leaves was not measured. The high litterfall in the thickets without *Clusia* compared to *Clusia* thickets may be a result of the spatial variation in

floristic composition and structure in the open *Clusia* formation in this restinga (Pimentel *et al.* 2007, Pereira & Araújo 2009), which occupies a large area with distinct characteristics of soils and water availability that may result in a complex system dynamics.

It is known that litterfall production is driven by a pool of different factors such as floristic composition and successional stage of the vegetation (Villela & Proctor 1999, Vitousek 2004, Saiter *et al.* 2009, Camara *et al.* 2018), that explains the variation in litter productivity among vegetations types. The annual litterfall production in the HCT in the present study was higher than in thickets with and without *Clusia* in other studies (Brito *et al.* 2018) and in the lower range reported for restinga forests (Ramos & Pellens 1993, Moraes *et al.* 1999, Pires *et al.* 2006, Brito *et al.* 2018). It is important to highlight that the restinga forest is a complex ecosystem in terms of floristics and structure (Ramos & Pellens 1993, Araújo & Pereira 2009) with a higher biomass (Dias *et al.* 2006), so a higher productivity in those formations than in the thickets was expected.

The seasonal pattern of litterfall mass and input of all nutrients through litterfall in both *Clusia*

thicket types showed a peak in the dry season as has been reported in other studies in the restinga (Ramos & Pellens 1993, Moraes *et al.* 1999, Brietz *et al.* 2005, Pires *et al.* 2006, Brito *et al.* 2018, Gripp *et al. in press a*). Many cases have been reported where the peak of litterfall and nutrient input occurs in the dry season, for example in semi-deciduous Atlantic forest of southeast Brazil (Pagano 1989, Louzada *et al.* 1997, Villega *et al.* 1998, 2006, 2012) and Amazon (Villega & Proctor 1999); and in other tropical forests elsewhere (Saiter *et al.* 2009). The seasonal behavior of leaf litterfall and the influence of precipitation deficits and high temperature to regulate leaf litter production in the open *Clusia* formation in the Jurubatiba Restinga, has been discussed elsewhere in this volume (Gripp *et al. in press a*), suggesting that annual leaf litterfall is less affected by precipitation regimes than temperatures probable due to the CAM photosynthesis dominant species, *C. hilariana*, which may avoid water stress. Nevertheless, according to these authors, only 15 % of those seasonal variation was explained by climate, indicating that most variation of the litterfall in open *Clusia* formation is driven by other factors, such as species diversity and clump structure (Gripp *et al. in press a*).

One of the consequences of the successional stage of the thickets was the higher Mg concentrations in the HCT litter as a result of the leaf-litter concentration. This fact may be related to a possible high photosynthetic rate of those adult healthy trees and less sclerophylly as reported for other successional vegetation (Camara *et al.* 2018). Besides that, the lower Na concentration of *C. hilariana* leaf-litter in the HCT than in the SCT seems to be a response to its lower concentration in those soils. A positive correlation between concentrations of Ca, Mg and Na in leaves and soils was found in a restinga in the Barra de Maricá, RJ (Henriques & Hay 1992). Sea salt spray, rich in cations such as Na, K and Mg, is an important source of nutrient in restinga ecosystems (Hay & Lacerda 1984). Therefore, the higher concentrations of Na in SCT soils may be related to a greater Na input through salt spray, as SCT canopy openness is higher compared to HCT, allowing Na deposition on the soil surface. It was observed that the presence of nurse plants reduced the salinity of soils compared to an adjacent open area of an arid ecosystem (Navarro-Cano *et al.* 2019), that may be

one of the roles of *Clusia* when it reaches a high canopy coverage as in the HCT.

The C and N concentrations in the litterfall did not differ between thicket types in the present study nor in the ones studied by Brito *et al.* (2018) in the same restinga. *Clusia* leaf-litter had a lower N concentration and higher C/N ratio than in the other leaves fraction, as detected in its green (Silva 1999) and senescent (Dias 2008, Brito 2018) leaves. Thus, the low N concentration in *C. hilariana* leaves might be due a limitation of nutrients in the restinga ecosystems, as was reported for other vegetation types dominated by one species (Haghverdi & Kooch 2019). But, regardless of the fact that *Clusia* leaf-litter had low N concentration, N inputs via its litterfall was high as a consequence of the large amount of its leaf-litterfall, resulting in a greater input of N and other nutrients in the HCT than in the SCT, corroborating the second part of hypothesis 2. This highlights this species' importance in restinga nutrient input and gives support of *C. hilariana* as an important species in the successional process of this ecosystem.

The higher decomposition rate in the HCT than in the SCT in the first year of the experiment (373 d) was expected in hypothesis 3, since in the beginning of the decomposition process the most labile fractions in the organic matter are released and mineralized (Swif & Anderson 1989). During this period the decomposing material is more susceptible to environmental effects, such as temperature and humidity acting as key drivers of organic matter decomposability. Some measurements of temperature and humidity below the thickets in the first year of the study showed that the HCT had higher soil humidity and lower temperatures (Bonadiman 2007), that might have positively affected a faster mass loss of *Clusia* leaves there. However, after that period, until the end of the experiment, the mass loss was similar between thickets when it is probable that more recalcitrant materials were decomposed more slowly and were more affected by microbial activity than by abiotic factors (Swif & Anderson 1989, Riggs *et al.* 2015). Microbes were cited as the main biota to act as decomposers in thickets with *Clusia* in this vegetation formation, while fauna was for the most labial material of other leaves under thickets without *Clusia* (Brito *et al.* 2018).

The annual decomposition rates of *C. hilariana*

leaf-litter (0.29) in both the HCT and the SCT was higher than values obtained for this species (0.25, Dias 2008) and for mixed leaf-litter (0.24, Brito *et al.* 2008) in other thickets in this open *Clusia* formation. However, the present research was carried for a longer period and *C. hilariana* leaves reached 58 to 53 % of mass loss at the end of the experiment (1059 days). In another decomposition experiment made with leaves of other species in Jurubatiba Restinga thickets Dias (2008) reported that *C. hillariana* and *Eugenia umbelliflora* ($k = 0.24$, non-dominant) leaves decomposed slower than leaves of another dominant tree, *Protium icariba* ($k = 0.37$), but with a nonsignificant difference among them. Even though when the effect of the species composition on decomposition process was evaluated for these dominant species, there was a positive relation between the composition of the dominant species and the litter quality, indicating that the dominant species influence on decomposition is more due to its change on litter quality (Dias 2008, Gripp *et al. in press b*). A recent review on the decomposition studies in the Jurubatiba National Park (Gripp *et al. in press b*) stated that litter quality is one of most important drivers on the restinga litter decomposition process.

Leaf litterfall high in lignin (Silva 1999) and low in N, as recorded for *Clusia*, is reflected in low decomposition rate and N immobilization (Dias 2008, Rigg *et al.* 2015). High C/N values in the leaf litter express N limitation for decomposers which immobilize N (Vitousek *et al.* 1982, Hobbie 2015, Rigg *et al.* 2015). These factors may explain the low decomposition rates obtained for *Clusia* leaves in this study and others (Dias 2008, Gripp *et al. in press b*). Therefore, although *C. hilariana*'s contribution to N cycle in these thickets seems contradictory, as its input throughout leaf-litter is high and its releases to the soils through litter decomposition process to become available is slow, this strengthens the role of this species in the conservative mechanism of nutrient cycling, known as essential to the maintenance of plants (Hay & Lacerda, 1980, 1984, Vitousek 1982) in sandy oligotrophic soils (Brito *et al.* 2018), especially for N that is one of the most limiting nutrients in dry environments. But, Brito *et al.* (2018) considered that N loss from mixed leaf-litter was even higher in thickets with *Clusia* than those without, that according to the author, promotes plant N uptake in these thickets.

In general, there were not many differences in the release of most nutrients between both thicket types (Bonadiman 2007). With the exception of K that was easily leachable in the HCT in accordance with hypothesis 3 (Figure 5). Nutrient release was not directly influenced by mass loss of *Clusia* leaf-litter during decomposition process (Bonadiman 2007). It is interesting to note that K concentration in other leaves of the litterfall was also higher in the HCT, and this litter fraction was higher in K than *C. hilariana* leaves. It is known that K might be of great importance for the survival of plants under environmental stress conditions, such as drought, suggesting that it may be a strategy for other species in those thickets to survive in this dry ecosystem. But it was not reflected in an increase in K availability in the HCT soil, probably due to the low contribution of other leaves in these thickets total litterfall and to the leachable characteristic of this ion. Sodium showed a net release in both thickets, probable as consequence of its high concentrations in *C. hilariana* leave that was up to twice greater than in other leaves.

Soil chemistry did not reflect more nutrient input through *Clusia* leaf-litter, as it was similar among thickets not corroborating hypothesis 1 of this study, as found in other thickets studied in this restinga (Brito *et al.* 2018). Nevertheless, it may be a consequence of a slow nutrient release from *Clusia* leaves, and even possibly an immobilization mechanism reported as a negative feedback in plant nutrient cycling rates that may occur (Hobbie 2015). However, as stated by Hobbie (2015) it is important to have a more careful look at the decomposition process to move beyond assessments of leaf-litter feedbacks to a broader understanding of what was called whole-plant litter. It will be essential to have a better understanding of how species affect nutrient cycling (Hobbie *et al.* 2015) and possibly creates feedback in these thickets.

Taking into account the evidences obtained in this long term study, we may consider *Clusia hilariana* to be a key species in the nutrient dynamics in this formation at Jurubatiba Restinga National Park, due to the considerable contribution of its leaves to the total organic matter and input of nutrients to the system and the slow decomposition and nutrient release of their leaves. *Clusia* has a high biomass in the Jurubatiba Restinga (Dias *et al.* 2006), that reinforces the suggestion of its strong effect on

productivity and nutrient cycling in this ecosystem (Dias & Scarano 2007, Brito *et al.* 2018). The role of nurse plants as key engineers in abiotically stressful ecosystems has been investigated and confirmed for some arid environments where biomass and biodiversity effect through an increment in litter production promoted plant-microbe interactions in this arid system (Navarro-Cano *et al.* 2019). According to these authors, this result changed the idea of facilitated species being simple beneficiaries of the nurse's effects, turning them into co-drivers of an essential ecosystem function.

Canopy influences on the litter input and nutrient cycling have been emphasized in forests (Prescot 2002) and arid ecosystems (Navarro-Cano *et al.* 2019). This pattern, of one species being related to a strong influence on nutrient cycling through its productivity and nutrient cycling has been shown elsewhere, for example for *Peltogyne gracilipes* in a monodominant Amazon forest (Villega & Proctor 1999, Villega & Proctor 2002), *Metrodorea nigra* in a seasonally dry Atlantic forest (Villega *et al.* 2006) and *Fagus orientalis* in a beech forest in Iran (Haghverdi & Kooch 2019). Litterfall mass and nutrient inputs have shown to be better predictors of the effect of tree species on nutrient cycling than decay rate (Prescot 2002). This was the case for *Clusia hilariana's* influence on the thicket formation in the study area since decomposition rate and most nutrient release were not so clearly affected by its successional stage, as were litterfall mass and its nutrients. Studies with other species in restinga, relating their presence with soil quality, suggested that *Neoregelia cruenta* (Hay & Lacerda 1980), *Protium icicariba* and *Allagoptera arenaria* (Menezes *et al.* 2000) may be contributing to a change in soil nutrient quality and so may be acting as nurse plants in restinga ecosystems. These are crucial mechanisms that should be better investigated in restinga ecosystems.

This long term study gave an important opportunity to study on the role of *C. hilariana* in nutrient cycling as a key species on the open *Clusia* scrub formation in the Jurubatiba Restinga National Park, PELD Site 5, that is not easily obtained in short term studies due to the duration of the processes, such as *Clusia* leaf decomposition. The hypothesis that *Clusia hilariana* acts as a key species, promoting an improvement in nutrient cycling according to its presence and senescence, was

corroborated for most nutrient cycling processes assessed. *Clusia* leaf-litter was determinant for high organic matter availability, nutrient input, and decomposition via its litter, which decreases according to *Clusia* senescence. Furthermore, the slow litter decomposition and nutrient release from *C. hilariana* leaf-litter may be an important mechanism of nutrient conservation as suggested for restinga ecosystems (Hay & Lacerda 1984, Brito *et al.* 2018, Gripp *et al. in press b*). Thus, the results suggest that *C. hilariana* may act as a nurse plant in relation to the nutritional dynamics of the thickets dominated by this species in the open *Clusia* formation in the Jurubatiba National Park. Nevertheless, more comprehensive researches on the role of *Clusia hilariana* promoting additive effects on soils, productivity and nutrient cycling mechanisms, should be experimentally investigated in long term studies to more clearly elucidate the knowledge of this species as a facilitator-driven in this ecosystem.

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Supplementary Material: Table 1. Litterfall ($t\ ha^{-1}yr^{-1}$) from Jurubatiba Restinga National Park, RJ, Brazil. Values for means and standard deviations for three traps in each thicket type: healthy *Clusia* thickets (HCT, N = 6), senescent *Clusia* thickets (SCT, N = 6) in each of the seven consecutive years. The uppercase letters within a row (**A** and **B**), indicate significant differences (One-Way-ANOVA- $p < 0,05$) between the thicket types, for each fraction. The lowercase letters within column (**a**, **b**, **c**, **d**, **e**, **f**, **g**) indicate significant differences among fractions within each thicket type (ANOVA- $p < 0,05$).

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