



## Ultrastructural and functional chloroplast changes promoting photoacclimation after forest management in a tropical secondary forest

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### ARTICLE INFO

#### Keywords:

Atlantic forest  
C isotopes  
Gas exchange  
Leaf traits

### ABSTRACT

Forest management involving the selective logging of exotic species in order to reestablish native flora alters microclimatic conditions and selects for species with heightened capacity to adapt to the new conditions. This study investigated whether, after forest management involving the removal of eucalyptus, ultrastructural adjustments in the chloroplast fostered the photoacclimation of the most abundant regenerating native species in a Brazilian Atlantic forest biological reserve. The influence of seasonality on photosynthetic activity and water use efficiency after the forest management was also assessed. To achieve this, in the rainy season mature leaves of native tree saplings (*Xylopia sericea*, *Siparuna guianensis*, and *Byrsonima sericea*) were subjected to ultrastructural analyses and the C isotopic composition ( $\delta^{13}\text{C}$ ) was determined; and in the dry and rainy season gas exchange and chlorophyll *a* fluorescence were measured. Species samples were obtained in: secondary forest, a eucalyptus understory with 15 years of regeneration before and 12 months after the management, and from herbarium samples from eucalyptus understories collected at the beginning of forest regeneration (9–16 years ago, for  $\delta^{13}\text{C}$  analyses only). Ultrastructural alterations such as the reorganization of thylakoids, starch grain changes, and the presence of plastoglobules and oils were verified after the management in all the species.  $F_v/F_m$  values varied between 0.80 and 0.90 regardless of the management or season of the year. There was a reduction of C assimilation after the management, especially in the dry season.  $^{13}\text{C}$  enrichment was observed for *B. sericea*, *S. guianensis*, and *X. sericea* in herbarium samples (−31.4‰, −32.0‰, and −31.4‰, respectively) and after the forest management (−31.2‰, −32.5‰, −31.4‰), while samples depleted in  $^{13}\text{C}$  were registered before the management (−33.4‰, −33.3‰, −33.2‰) and in the secondary forest (−34.0‰, −33.9‰, and −33.6‰). The data suggest that ultrastructural alterations may have aided in maintaining electron flow after the increase in irradiance due to the forest management, avoiding photochemical stress, as evidenced by  $F_v/F_m$  values. The forest management increased the efficiency of water use and fostered abiotic conditions similar to those present at the beginning of the understory regeneration. These previous conditions favored the current high level of abundance of these three species, highlighting the importance of monitoring to ensure that the management practices do not promote the future dominance of few species at the expense this biome's high biodiversity.

### 1. Introduction

Anthropogenic activities in forest environments can involve practices such as burning, the establishment of forest pasture, agriculture conversion, enrichment from the planting of native species, the removal of exotic species, the partial removal of native species for agroforestry systems, and the sustainable exploitation of natural resources (Holl and Aide, 2011; Rolim et al., 2017; Vitoria et al., 2016). The secondary

forests resulting from such human interventions have become increasingly common landscape features, representing approximately 60% of the world's forests in 2005 (FAO, 2005). However, efforts to increase the area of vegetable coverage worldwide have led to an increase in the area of planted forests, representing approximately 7% of the world's forests (FAO, 2010). Secondary or planted forests are important reserves of biodiversity that provide ecological services such as carbon sequestration (Bongers, 2015; Morellato and Haddad, 2000; Thompson

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et al., 2012). The primary productivity of secondary forests is generally 3–5 times higher to that of primary forests even though their stocks of C are comparatively lower than those of intact forests (Lewis et al., 2009; Luysaert et al., 2008). This is possibly a consequence of the higher leaf turnover that occurs in secondary forests when compared with primary ones, since more acclimation processes take place in ecosystems undergoing restructuring (Vitousek and Matson, 1984).

Efforts aimed at preservation, the connecting of fragments, and forest recomposition have been employed with regard to secondary forests (Abreu et al., 2014; Rolim et al., 2017). In Brazil, degradation and fragmentation of the Atlantic forest continue to represent consequences of the encroachment of agricultural and cattle-raising activities, urban areas, and industrial growth (Cabral and Fizon, 2004). This biome is currently restricted to less than 15% of its original area, including relatively small forest remnants, of which 83.4% are under 50 ha (Ribeiro et al. 2009). Even remnants protected by law contain exotic species or situations requiring forest management. In one such reserve, the União Biological Reserve in Rio de Janeiro State, the removal of eucalyptus (*Corymbia citriodora*) altered the microclimate of the understory, consequently affecting the performance of regenerating native species (Lage-Pinto et al., 2015; Silva et al., 2010; Teixeira et al., 2015; Vitoria et al., 2016). This scenario has required photoacclimation adjustments from the species that remained after the forest management. The microclimatic alterations caused by this intervention modified the isotopic signature of C in the chief understory regenerative species, causing photochemical stress in young leaves, and accelerating physiological maturity (Vitoria et al., 2016). However, mature leaves are more tolerant to the environmental variation than the young ones and, under certain conditions, these mature leaves showed an increase in C assimilation (Teixeira et al., 2015; Vitoria et al., 2016). It is still not known which mechanisms have contributed to the photoacclimation and continued presence of the native understory species after the forest management.

Leaves exposed to higher irradiance generally present lower specific leaf area (SLA), increased thylakoid stacking, and higher numbers of plastoglobules when compared to shaded leaves (Lichtenthaler et al., 1981; Vitoria et al., 2016). The main function of these alterations is to maintain photosynthetic conditions, in light of the fact that an excess of irradiance can culminate in photoinhibition, reduced C assimilation, and reduced photosystem II quantum yield (PSII) (Araújo and Deminicis, 2009; Demmig-Adams et al., 1996). The photoinhibition can be reversible or irreversible depending on the amount of time and intensity that the irradiance exceeds the photon absorption capacity of the PSII (Adir et al., 2003; Ort, 2001; Osmond, 1994). Factors combined with excessive irradiance, such as hydric restriction and increased VPD, can promote a drastic reduction of photosynthetic capacity, contributing to the occurrence of photoinhibition processes (Kitao et al., 2000; Lemos Filho et al., 2004). In general, plants under conditions of excessive irradiance and hydric limitation reduce stomatal conductance ( $g_s$ ) decreasing  $^{13}\text{C}$  discrimination, resulting in structures enriched in  $^{13}\text{C}$  (Farquhar et al., 1989).

Therefore, this work assessed the spatial-temporal effects of the forest management characterized by selective logging of eucalyptus (*Corymbia citriodora*) with regard to the photoacclimation capacity of the three main regenerating native species (*Xylopia sericea*, *Siparuna guianensis*, and *Byrsonima sericea*), while seeking answers to following questions: (1) Do ultrastructural adjustments in chloroplasts aid in the photoacclimation of these species after the selective logging of eucalyptus? (2) Is there a synergistic effect between the dry season and management on photosynthetic performance? (3) Was there temporal influence by the management on the  $\delta^{13}\text{C}$  of the regenerating understory species (herbarium and current samples)? The authors hypothesized that (1) ultrastructural alterations would assist the species in photoacclimation, avoiding post-management photoinhibition processes, (2) reductions in C assimilation and stomatal conductance would occur after the management in the dry season (3) herbarium

**Table 1**

Characterization of the study areas (secondary forest; before eucalyptus removal; after eucalyptus removal) in the União Bio Reserve, in January 2013 and February 2014. – not applicable.

	Secondary forest	Before	After
Mean irradiance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) <sup>a</sup>	9	506	1480
Presence of eucalyptus	No	Yes	No
Spacing of eucalyptus trees (m)	–	1.5 × 3	–
Distance to the secondary forest (km)	–	1.5	1.5
Management duration (months)	–	–	12
Eucalyptus removal management	No management	No management	Yes
Understory conditions developed	Dense vegetation	Well-developed vegetation	Sparse vegetation

<sup>a</sup> Values obtained at 1.30 m in 30 points between 1100 AM and 100 PM on a sunny day using a quantum sensor (*Li-190* coupled to *Li-250 A*, *Li-Cor*, USA).

samples, collected between 9 and 16 years ago in the regenerating understories of the eucalyptus, would be enriched in  $^{13}\text{C}$  in comparison to the current samples.

## 2. Materials and methods

### 2.1. Study area, species, and sampling season

The present study was carried out in a secondary Atlantic forest section and an area formerly planted with eucalyptus (*Corymbia citriodora* (Hook.) K.D. Hill & L.A.S. Johnson) before and after forest management in the União Biological Reserve, Rio de Janeiro State, Brazil (22°27'S, 42°02'W) (Table 1, SM 1). The reserve contains approximately 7800 ha, of which 220 were planted with eucalyptus before they were clear-cut. The climate of the region is tropical humid Aw (Alvares et al., 2013), with an annual average temperature of 25 °C and average annual precipitation of 1900 mm (85% occurring between October and April). The planting of eucalyptus took place in 1967 and the silvicultural practice of removing the native species understory was discontinued in 1996. The collection of data and botanical material was performed before and after the removal of eucalyptus during the rainy season (February 2013 and January 2014, respectively) and during the dry season (May 2013 and June 2014, respectively).

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.06.032>.

The most abundant species were selected (Evaristo et al., 2011): *Siparuna guianensis* Aubl. (early secondary tree), Siparunaceae, *Xylopia sericea* A. St.-Hil. (pioneer tree), Annonaceae, and *Byrsonima sericea* D.C. (pioneer tree), Malpighiaceae (Lorenzi, 2000). Study individuals height ranged from 1.5 to 2.5 m. These species were also assessed using herbarium material collected from the same eucalyptus plantation in 2000 (*Siparuna guianensis*), 2001 (*Xylopia sericea*), and 2007 (*Byrsonima sericea*), and bear the HUENF registration numbers of 6307, 1641, and 3850, respectively. From five to seven samples per species were collected.

### 2.2. Transmission electron microscopy (TEM)

Fragments from the middle third of leaves of the three species collected in January 2013 (before management) and December 2014 (after management) in each area (Table 1) were fixed in the field in a solution containing 2.5% (v/v) glutaraldehyde and 4.0% (v/v) paraformaldehyde in 0.05 M sodium cacodylate buffer (pH 7.2). Subsequently, the samples were rinsed and post-fixed for 2 h at room temperature with 1.0% (v/v) osmium tetroxide with the same buffer, for 1 h. Samples

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