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Biochemical leaf traits as indicators of tolerance potential in tree species from the Brazilian Atlantic Forest against oxidative environmental stressors

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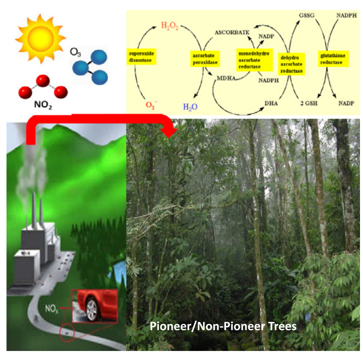
HIGHLIGHTS

- We established the tolerance potential of trees from the Brazilian Atlantic Forest.
- The functional approach was used to achieve a higher relevant evaluation.
- Leaf antioxidants and oxidative injury were analyzed in pioneer/non-pioneer trees.
- Pioneer trees were more tolerant against oxidative stress than non-pioneer species.
- The biochemical leaf traits varied in response to combined environmental stressors.

GRAPHICAL ABSTRACT



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ABSTRACT

The tolerance potential against the oxidative injury in native plants from forest ecosystems affected by environmental stressors depends on how efficiently they keep their pro-oxidant/antioxidant balance. Great variations in plant tolerance are expected, highlighting the higher relevance of measuring biochemical leaf trait indicators of oxidative injury in species with similar functions in the forest than in single species. The use of this functional approach seems very useful in the Brazilian Atlantic Forest because it still holds high plant diversity and was the focus of this study. We aimed at determining the tolerance potential of tree species from the Atlantic Forest remnants in SE Brazil against multiple oxidative environmental stressors. We assumed that pioneer tree species are more tolerant against oxidative stress than non-pioneer tree species and that their tolerance potential vary spatially in response to distinct combined effects of oxidative environmental stressors. The study was carried out in three Atlantic Forest remnants, which differ in physiognomy, species composition, climatic characteristics and air pollution exposure. Leaves of three pioneer and three non-pioneer species were collected from each forest remnant during wet (January 2015) and dry periods (June 2015), for analyses of non-enzymatic and enzymatic antioxidants and oxidative injury indicators. Both hypotheses were confirmed. The pioneer tree species displayed biochemical leaf traits (e.g. high levels of ascorbic acid, glutathione and carotenoids and lower lipid peroxidation) that indicate their higher potential tolerance against oxidative environmental stressors than non-pioneer species. The biochemical leaf traits of both successional groups of species varied between the forest remnants, in response

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to a linear combination of oxidative environmental stressors, from natural (relative humidity and temperature) and anthropogenic sources (ozone and nitrogen dioxide).

1. Introduction

Forest ecosystems in the vicinities of human populations have been continuously subjected to multiple environmental stressors, from both natural and anthropic origins, such as climatic abnormalities (high sunlight radiation, extreme temperatures, water shortage) and high levels of ozone and other air pollutants (Tausz et al., 2007; Bussotti, 2008; Paoletti et al., 2010; Bussotti and Pollastrini, 2015). These environmental factors may induce oxidative stress in tree species as a result of increased production of reactive oxygen species (ROS) in plant cells (Gill and Tuteja, 2010; Sharma et al., 2012; Contin et al., 2014). However, the tolerance potential shown by plant species against the oxidative injury will depend on how efficiently they mobilize antioxidant defenses, keeping the pro-oxidant/antioxidant balance. Several non-enzymatic substances (e.g. carotenoids, ascorbic acid, glutathione) and enzymes (e.g. superoxide dismutase, catalase, ascorbate peroxidase and glutathione reductase) are well-established antioxidants (Iriti and Faoro, 2008; Gill and Tuteja, 2010; Foyer and Shigeoka, 2011; Foyer and Noctor, 2013; van-Doorn and Ketsa, 2014). The leaf levels of other pigments (for example, chlorophylls) and derivatives of lipid peroxidation (for example, hydroperoxide conjugated diene) may add key information on the susceptibility of plants to natural and anthropogenic oxidative stress (Pignata et al., 2002; Gratão et al., 2012).

Plant species from forest ecosystems present great variations in tolerance against multiple environmental stressors. This fact highlights the higher relevance of measuring antioxidants and other biochemical leaf trait indicators of oxidative injury in species with similar functions in the forest than in single species chosen by other criteria. Paoletti et al. (2010) commented that a future challenge is the better understanding of how genes determine physiological plasticity, adaptation and survival of tree populations to climatic factors and air pollutants. We may assume that this challenge is even greater in tropical/subtropical forest ecosystems, such as the Atlantic Forest that still remains in southeast Brazil. This biome holds high species richness and rates of endemism. However, it is among the tropical ecosystems at risk of extinction, being one of the hotspots for biodiversity conservation (Groeneveld et al., 2009; Ribeiro et al., 2009; Freitas et al., 2010; Lira et al., 2012). Most of the remaining Atlantic Forest in southeast Brazil exists in small fragments and has been affected by diverse environmental stressors, such as climatic abnormalities and air pollutants emitted by large metropolitan conglomerations, industrial centers and extensive agricultural lands. Therefore, all scientific knowledge that contributes to preserve these forest remnants is welcome (Esposito and Domingos, 2014; Domingos et al., 2015; Esposito et al., 2016; Pedroso et al., 2016).

The use of the functional approach may overcome the abovementioned challenge (Bassin et al., 2007; Bussotti and Pollastrini, 2015). It has been applied in some studies, like in Salvatori et al. (2014), which assessed different plant functional groups (evergreen and deciduous woody and herbaceous plants) subjected to stresses caused by different abiotic conditions (drought, salt, ozone, UV radiation). Bussotti et al. (2015) investigated the adaptive capacity of European forests to climate change by using functional traits for selecting adapted genotypes to drought, for example, to be used in forest management.

Besides, Bussotti (2008), based on a review about the functional leaf traits in native species from Mediterranean forests, concluded that early successional species have a lower tolerance against oxidative stress than the late secondary species. In contrast, Favaretto et al. (2011) classified the tropical tree species into two major functional groups, based on the tolerance against solar radiation exposure: the pioneer species that are tolerant to high solar radiation and then theoretically more tolerant to oxidative stress and the non-pioneer species that are adapted to shading and possibly less tolerant to oxidative stress. Aguiar-Silva et al. (2016), by evaluating for the first time antioxidant responses of a few number of tree species from the Atlantic Forest, appeared to reinforce the assumptions of Favaretto et al. (2011). These first results stimulated the present further study, with aimed to determine the tolerance potential of tree species from the Atlantic Forest remnants in SE Brazil against multiple oxidative environmental stressors, using the mentioned functional approach. We raised the following hypotheses: 1) pioneer tree species are more tolerant against oxidative stress than non-pioneer tree species and 2) The tolerance potential of both functional groups vary between the Atlantic forest remnants in response to distinct combined effects of oxidative environmental stressors. They were tested by: 1) describing key biochemical leaf traits associated to oxidative stress in representative pioneer and non-pioneer trees species from the Atlantic Forest and 2) determining spatial variations in the biochemical leaf traits and possible oxidative environmental stressors that induced those variations.

2. Material and methods

2.1. Atlantic Forest remnants description, tree species selection and sampling procedures

The Atlantic Forest in São Paulo State (SE Brazil) is composed of distinct vegetation physiognomies, mainly determined by climatic and altitudinal gradients established between the Atlantic coast and interior of the State. Although they have distinct plant communities, all of them are highly diverse in species. The disorderly and intense land occupation by metropolitan conglomerations, industrial centers and extensive agricultural lands have promoted intense fragmentation of the Atlantic Forest in São Paulo, as well as the environmental contamination by pollutants (Groeneveld et al., 2009; Ribeiro et al., 2009; Freitas et al., 2010; Lira et al., 2012; Domingos et al., 2015). The leaf samplings were carried out in three Atlantic Forest remnants protected by Conservation Unities - [Municipal Park Paranapiacaba (PP); State Park Fontes do Ipiranga (PEFI) and Ecological Area of Relevant Interest Mata de Santa Genebra (MSG)]. They are located in increasing distances from the edge of the Paulista Plateau (Fig. 1), differing in physiognomy, species composition and climatic characteristics, such as rainfall amounts and seasonality, relative humidity and air temperature. They are also subjected to air pollution from distinct emission sources (Table 1). The forest remnant included in the Municipal Park Paranapiacaba was taken as the reference because it has been less affected by air pollutants and climatic seasonality, which are known oxidative environmental stressors.

The choice of tree species in each forest remnant was based on the functional approach and on the passive biomonitoring with native species related by Franzle (2003) and, when possible, on the taxonomic similarity. Three pioneer species and three non-pioneer species were selected (Table 2), among the most representative species in each conservation unit indicated in previous floristic surveys (PP: Lima et al., 2011; PEFI: Tanus et al., 2012; MSG: Guaratini et al., 2008).

The leaf samples of each tree species were collected during the wet (January 2015) and dry periods (June 2015). The sampling procedures were replicated once a day (between 10 h a.m. and 12 h) in five consecutive days per period, from four to six trees per species with circumference at the height breast ≥30 cm. We collected at least ten leaf samples from four to five branches of each tree that were located eight to twelve meters above ground level and fully exposed to the sunlight. Immature